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SERIE: PLANKTON · BIND V

Nr. 4. E. Steemann Nielsen: THE MARINE VEGETATION OF THE ISEFJORD — A STUDY ON ECOLOGY AND PRODUCTION

KØBENHAVN
C. A. REITZELS FORLAG
BIANCO LUNOS BOGTRYKKERI
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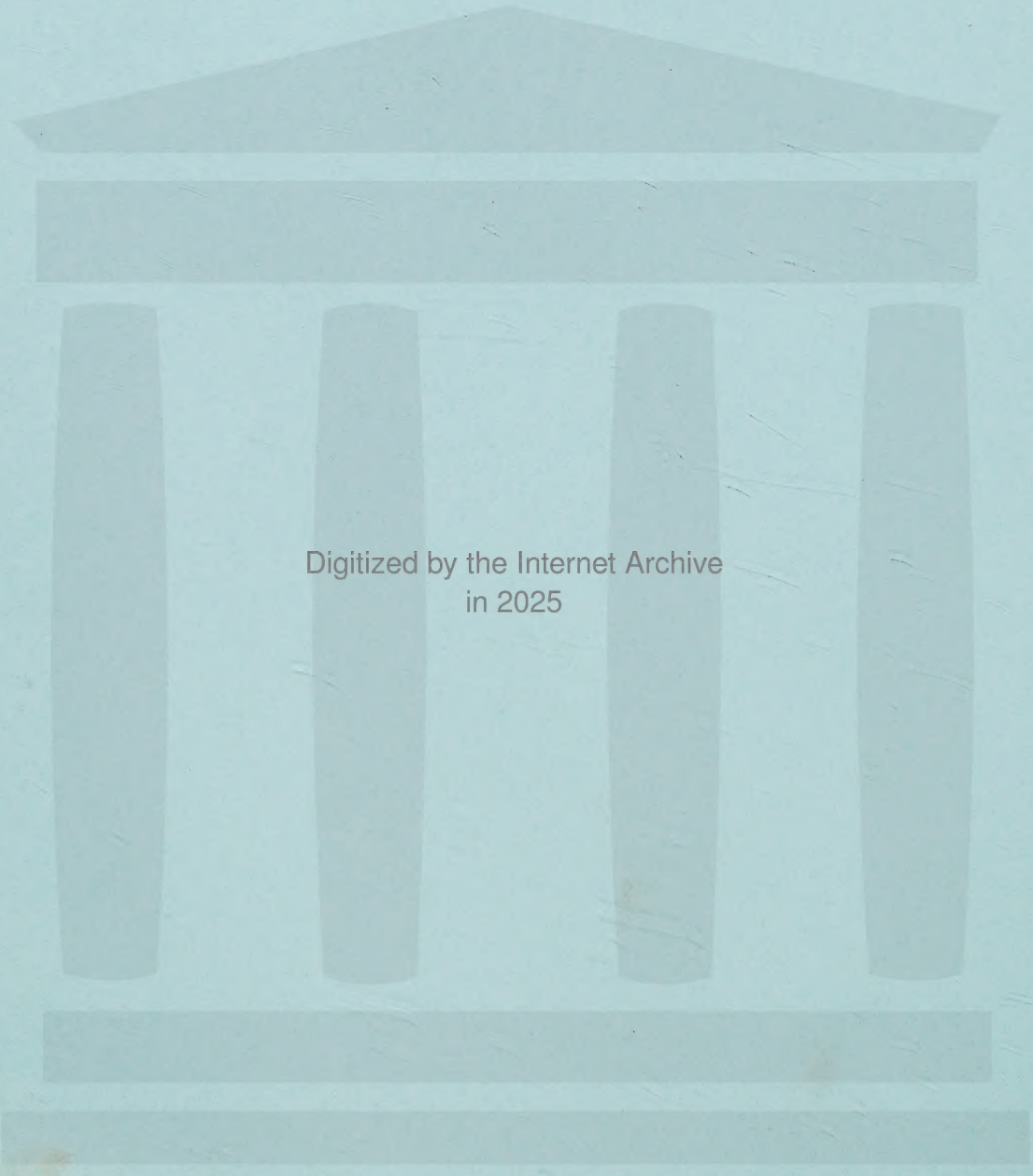

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FOR DANMARKS FISKERI- OG HAVUNDERSØGELSER

SERIE: PLANKTON · BIND V · NR. 4 · 1951

THE MARINE VEGETATION OF THE ISEFJORD

A STUDY ON ECOLOGY AND PRODUCTION

BY

E. STEEMANN NIELSEN

WITH 47 TEXT-FIGURES

KØBENHAVN
C. A. REITZELS FORLAG
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1951

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PREFACE

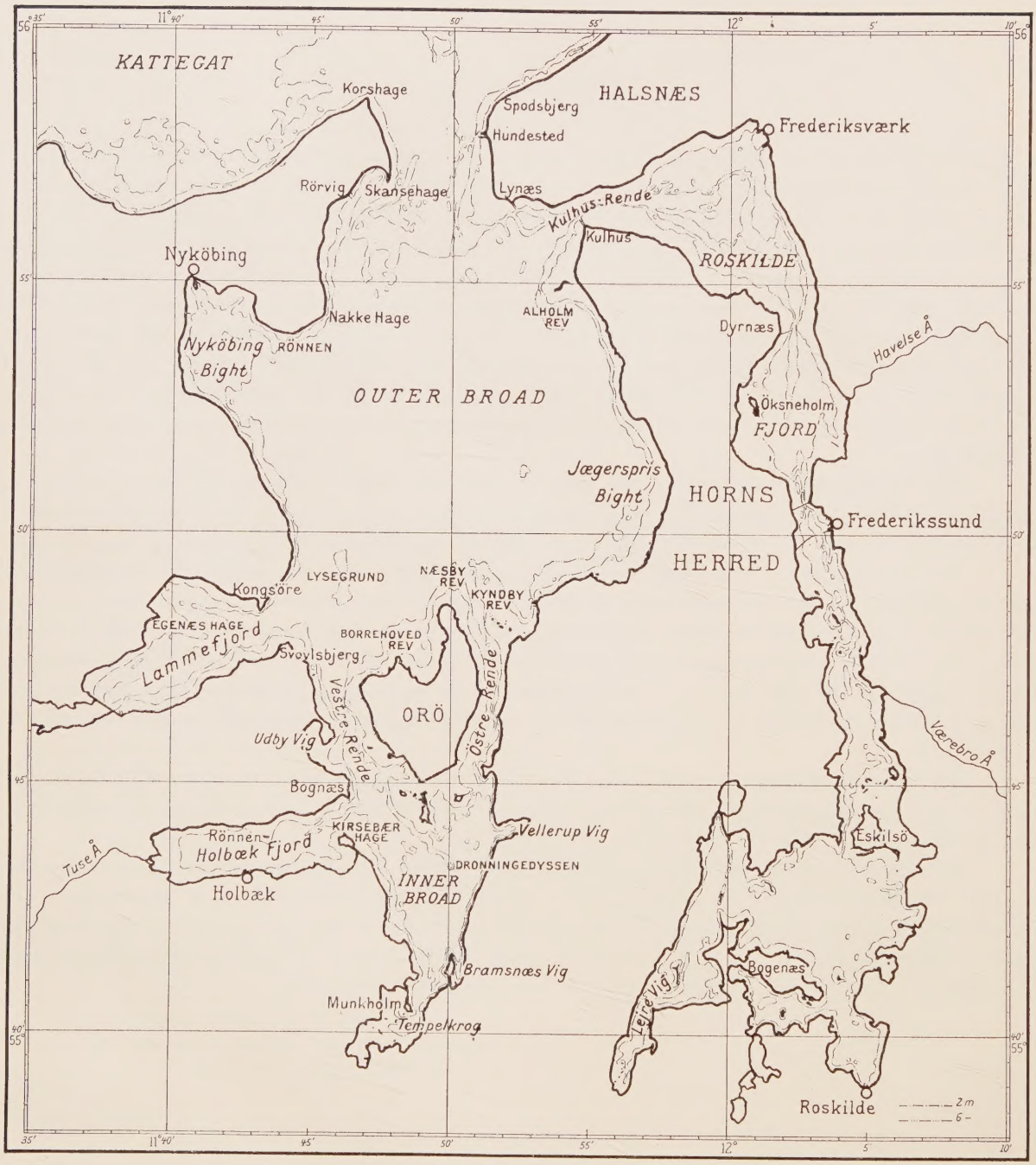
Marine biological investigations in the Danish waters were considerably impeded after the German occupation of Denmark in April 1940. Thus I had to discontinue some investigations of the production of plankton in the Great Belt which had just been started. So I decided to start investigations in a Danish fjord instead, and because of the comparatively short distance from Copenhagen I selected the Isefjord as the most suitable area. The late Professor Ove Paulsen, Ph. D., who was then director of the Plankton Laboratory of the Danish Committee for Fishery Investigations and the Study of the Sea, showed great interest in the matter. He provided valuable grants from the Carlsberg Foundation so that tasks outside the sphere of investigation of the Plankton Laboratory might be included in the investigations. A work by Dr. V. M. Mikkelsen 1949 is the result of investigations made in connexion with the main investigations.

Besides the investigations of the vegetation in the fjord which are to be published in the present paper, quantitative zooplankton samples were also collected. These collections have been treated by Dr. P. Jespersen, 1949, as regards the zooplankton proper.

The hydrographic investigations made in connexion with the biological investigations will be published in the introduction to the present paper. I offer my best thanks to Mr. H. Thomsen, head of the Nautical Department of the Danish Meteorological Institute, and to Mr. F. Hermann, M.Sc., of the Hydrographic Laboratory of the Danish Committee for Fishery Investigations and the Study of the Sea, for the great assistance given me, partly in the form of personal assistance, partly by having the majority of the chemical analyses made at the Hydrographical Laboratory.

The Danish Biological Station and the Ministry of Fisheries placed motor-boats at our disposal for the investigations, for which I offer my cordial thanks. I am especially obliged to Mr. K. Henriksen, fishery patrolman, of Hundested.

During the years 1941—1943 the main part of the investigations were made from the station "Bramsnæsvig" of the Danish Navy. I offer my respectful thanks to the Ministry for Naval Affairs, for permitting us to use the station as our base, and to the various chiefs of the station. Mine Quartermaster N. I. Andersen acted as assistant at the investigations made from the station. I am greatly obliged to him for his valuable assistance.



The Isefjord.

Chapter One

HYDROGRAPHY

A. Topography of the Isefjord.

The Isefjord stretches from the north coast of the Danish island of Zealand in a southerly direction (see the chart, p. 4, and Den danske Lods II, 1939). It covers an area of about 280 square km. (including the Roskilde Fjord about 400 square km.). The mouth of the fjord is about 4 km. in width. South of the mouth the fjord expands into a large basin, the Outer Broad, which is about 17 km. in length and about 13 km. in breadth. Nykøbing Bight and the Lammefjord (now about 8 km. long and 2 km. broad) debouch on the west side of the Outer Broad, and the narrow Roskilde Fjord, about 35 km. long, debouches on the east side.

South of the Outer Broad is the Inner Broad, about 7 km. in length and 4 km. in breadth, which is connected with the former through two rather narrow channels, Orø Vestre Løb and Orø Østre Løb, on either side of the island of Orø. The Holbæk Fjord (7 km. long, 2 km. broad) issues from the Inner Broad towards the west, Vellerup Vig and Bramsnæs Vig issue towards the east and Bramsnæs Bugt towards the south, continuing inside the peninsula Munkholm in Tempelkrog. The whole distance, as the crow flies, from the mouth of the Isefjord to the head of Tempelkrog is about 36 km. The Isefjord area developed during the Glacial Period. Pre-Quarternary formations nowhere reach the surface. In a few places the coast chiefly consists of postglacial formations.

The Isefjord is separated from the Kattegat by a typical threshold, although generally this is not of importance in a hydrographical respect because of the low depth in the fjord itself. In the mouth of the fjord there are two natural old shallow channels, Østerløb, with a depth of at least 2.7 m., and Vesterløb, with a depth of at least 3.1 m. Further, an excavated channel over the eastern part of the threshold, with a depth of 5.6 m., was opened in 1920. This channel in 1940 was deepened to 6.3 m. The width of this channel, however, is only 50 m.

The bottom outside the fjord in the east (off Spodsbjerg) slopes rather steeply, the 6-meter curve being situated about 400 m off the land, whereas the 6-meter curve is at a distance of 2400 m. from the coast at the western point (Korshage).

In the Outer Broad the depth is even, generally about 9 m. Along the coast there is a flat, often several hundred metres in breadth, with a depth of less than 2 m., and strewn with large stones. On the east side of the fjord, north of Jægerspris, the projecting shoal forms the large Alholm Rev (i. e. reef), on the middle of which the small island of Alholm is situated, surrounded by large stones, and south of this island the reef stretches further out about 1 km., with a depth of up to 2.5 m. On the southern side of the Outer Broad there are in several places reefs projecting far out, with less than 1 m. of water and large stones, which frequently are dry at low water. The most important of these reefs are Kyndby Rev, Næsby Rev, and Borrehoved Rev.

There are a few isolated shallows, first of all Lysegrund off the entrance to the Lammefjord. The type of bottom there is sand and stone as near the coasts. Otherwise the bottom in the Outer Broad consists of sand with an admixture of mud.

Both in Orø Østre Rende and Orø Vestre Rende the shallow water extends far out. In Vestre Rende there is a channel, 300 m. broad in the narrowest place, and with depths from 10 to 17 m. In Østre Rende the channel is narrow (in the narrowest place 60 m. broad, with depths of about 5 to 7 m.).

In the Inner Broad the depth outside the shallows is about 7 m. The shoal south of Orø is very broad, as a flat of sand projects there, on which there is a few minor islets. Some stones are found in several places on this flat, thus in the southernmost part, Dronningedyssen.

The shoal is quite narrow along the eastern coast of the broad, whereas it is fairly broad on the western side. In most places there are some smaller and bigger stones. In Tempelkrog the depth is nearly everywhere less than 2 m.

The bottom consists of mud everywhere in the Inner Broad outside the shallows. Whereas the bottom of the shallows in the east consists of regular sand (besides stones), it is in places on the western side somewhat mixed with mud. This is the case especially in Tempelkrog.

The shallow water in the Nykøbing Bight everywhere extends far out. A great many stones are found there. At the northeastern side of the bight the reef Rønnen, which consists of stones and has a depth of only 0.3 m., projects about 400 m. towards the south and slopes steeply to a depth of 5 to 6 m. The bottom outside the shallows consists of mud, and the greatest depth is 6 to 7 m.

In the Lammefjord the deep water at Kongsøre (the northeastern point) gets close to the coast, but the shallow water expands immediately inside it. From the middle of the north coast Egenæs Hage juts out about 2 km. It consists of sand and stones and has depth of 0.3—1.2 m. The large heap of stones Rønnen, which is dry at low water, is situated in the middle of it. The shallow water extends far out also on the south side of the Lammefjord, and in most places is very stony. Off the southeastern point (Svovlsbjærg) is the broad and stony Svovlsbjærg Rev with a depth of 3 m. as far as 1 km. from the shore. The bottom is muddy outside the shoals.

On both sides of the entrance to the Holbæk Fjord there are spits of land jutting far out and steeply sloping, on the southern side Kirsebærhage and on the northern side Sandhage. In the fjord the shallow water extends far out on both sides, on the northern side forming a flat, 1 km. in breadth, on which the small island of Rønnen is situated, surrounded by big stones. The greatest depth in the fjord is 6 m. The river Tuse Å debouches at the head of the fjord, which is here so shallow that the 4-m. curve is found about 3 km. from the mouth of the river. In the deep the bottom consists of pure mud, on the shallows of sand mixed more or less with mud and stones.

The fairly narrow entrance to the Roskilde Fjord, Kulhus Rende, is situated between Halsnæs and Horns Herred. The long fjord in a few places expands into broads, but long stretches of the fjord are narrow. The bottom in shallow water is stony nearly everywhere—thus the shallow on both sides of Kulhus Rende is covered with big stones—and slopes steeply from a depth of about 1 m. to 8—14 m. in the channel.

East of Kulhus Rende off Frederiksværk the fjord forms a broad full of shallows. Off Dyrnæs broad sandy hooks, sloping steeply towards the narrow but deep channel between them, project from both shores. South of this place the fjord expands again and forms a minor broad. On the western side are amongst others the small holm of Øksneholm.

South of this place the fjord is narrow for a length of 13 km. A few minor islands are found here. Farther south there is yet another broad with up to 6 m. of water. From this broad two creeks issue of which the one going south leads to Roskilde. In the creek towards the west we find the greatest depth in the whole Isefjord complex—24 m. This creek ends in the south in the very shallow Lejre Vig.

In the bottom in the Roskilde Fjord mud is found everywhere outside the shoals, whereas the bottom of shallow water is mostly sandy and often stony. However, it is somewhat mixed with mud in well protected places.

North and south of Frederikssund there are large bars of oyster-shells which originate from the Littorina period and which are dug out by excavators. The surface of these bars is mostly at depths of 1—2 m. Off Bognæs deposits of shells were found at a depth of 4 m.—presumably recent.

During the investigations the kinds of bottom in the various places were estimated, although only roughly. No mineralogical examinations of sediments were made, thus not one determination of the size of grains was made.

B. Hydrography of the Outer and the Inner Broad.

The Isefjord is connected with the Kattegat. As the depth on the threshold is only 3 m. (apart from the very small excavated channel in which the depth is just over 6 m.), only surface water from the southern Kattegat can penetrate into the fjord.

The mean salinity of the surface layer at the entrance to the fjord (off Rørvig) is 19.4 $^0/_{00}$ (according to daily measurements during the years 1895—1916 as listed in The Nautical-Meteorological Annual 1932). In winter the average salinity is highest (mean salinity for January 21.5 $^0/_{00}$). Table 1 shows all monthly means.

Table 1.

Mean salinities ($^0/_{00}$ S.) and temperature (°C.) according to daily observations at the surface at Rørvig 1895—1916 (according to the Nautical-Meteorological Annual 1932).

	$^0/_{00}$ S	°C
January	21.5	0.7
February	21.8	0.4
March	20.4	1.6
April	19.5	5.2
May	18.4	10.6
June	17.7	15.3
July	17.6	17.5
August	18.0	16.9
September	18.4	13.9
October	18.7	9.7
November	20.0	5.5
December	21.3	2.5
Year...	19.4	8.3

Table 2.

Mean salinities ($^0/_{00}$ S.) and temperature (°C.) according to daily observations at the surface at Schultz Grund 1903—1930 (according to the Nautical-Meteorological Annual 1932).

	$^0/_{00}$ S	°C
January	21.2	2.1
February	20.5	1.5
March	17.9	2.0
April	17.5	4.6
May	16.2	9.3
June	16.4	14.0
July	17.1	16.5
August	17.9	16.6
September	18.3	14.5
October	18.6	11.0
November	20.1	7.2
December	20.9	4.2
Year...	18.6	8.6

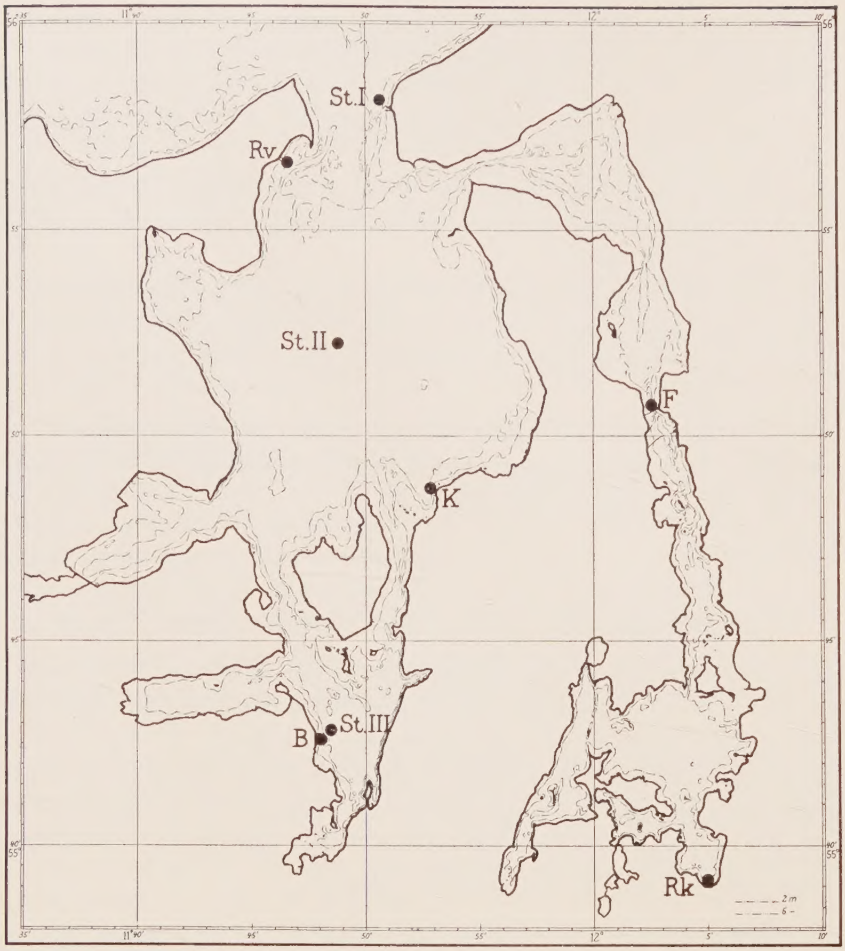


Fig. 1. Chart of hydrographic stations with daily observations (Rv = Rørvig, F = Frederikssund, K = Kyndby, B = Bramsnæsvig, Rk = Roskilde) and plankton stations (I—III).

The lowest salinity of the surface water in the Kattegat—both in the northern and southern part—is found in May, whereas the lowest salinity at the entrance to the Isefjord is found in July (the mean salinity at Rørvig in July is 17.6 $^0/_{00}$). The difference is due to conditions to be mentioned below. It can be stated that the neighbouring station of Schultz Grund in the Kattegat has an annual mean salinity of 18.6 $^0/_{00}$ (mean salinity for May 16.2 $^0/_{00}$). The monthly means are rendered in Table 2.

Besides the station at Rørvig at the entrance to the Isefjord the Meteorological Institute also has a permanent station in the Roskilde Fjord at Frederikssund, where daily measurements of surface salinity and temperature have been made since 1895.

In the period from Nov. 1st, 1942, to Oct. 31st, 1943, the Meteorological Institute in collaboration with the Danish Committee for Fishery Investigations and the Study of the Sea established similar stations at Kyndby Havn in the Outer Broad, the station of the Danish Navy "Bramsnæsvig" in the Inner Broad, and at Roskilde Havn in the Roskilde Fjord (see chart, fig. 1). Because of the internment of the Danish military and naval forces at the end of August 1943 salinity and temperature were not determined at the naval station in September and October

1943. On the other hand hydrographical observations were made at this station some once or twice a month during the period from March 1941 to September 1942 (Table 5). The observation material from the permanent stations for 1942—1943 is found in Table 3 (salinity) and Table 4 (temperature).

Table 3.

Mean salinities according to daily observations at the surface at stations in the Isefjord complex (Nov. 1942—Oct. 1943). According to the Nautical-Meteorological Annuals 1942 and 1943.

	Rørvig	Kyndby	Brams-næsvig	Frede-rikssund	Roskilde
November	20.6	21.1	..	17.9	15.1
December	21.1	20.3	20.8	17.2	14.6
January	20.5	21.5	22.1	..	12.6
February	21.3	20.0	21.2	17.0	12.6
March	21.3	21.6	21.2	16.3	12.6
April	19.1	19.1	20.8	18.2	12.9
May	18.8	20.0	19.7	17.3	13.9
June	17.3	18.6	19.3	17.8	14.2
July	17,9	18.3	18.4	18.2	14.7
August	17.4	17.6	18.0	17.9	14.7
September	18.0	17.3	..	16.4	14.7
October	18.2	18.1	..	16.0	14.9
Year	19.2	19.5	..	17.3	14.0

Table 4.

Mean values of temperature according to daily observations at stations in the Isefjord complex (Nov. 1942—Oct. 1943). According to the Nautical-Meteorological Annuals 1942 and 1943.

	Rørvig	Kyndby	Brams-næsvig	Frede-rikssund	Roskilde
November	6.3	6.1	..	5.0	5.5
December	2.9	3.0	2.8	1.5	2.2
January	0.4	0.3	0.3	..	0.2
February	2.8	2.7	2.7	2.8	2.8
March	3.5	3.8	4.1	4.2	4.3
April	7.5	7.7	7.0	7.7	8.1
May	11.8	11.7	12.5	13.1	12.8
June	17.2	15.5	16.4	18.0	16.0
July	18.4	18.1	18.5	19.4	18.9
August	17.0	16.9	17.8	17.7	17.5
September	10.4	14.5	..	11.5	15.3
October	10.6	10.5	..	10.4	10.8
Year	9.0	9.2	..	10.1	9.1

Furthermore, in 1940—1943 the salinity was determined on various excursions through the fjord. Thus we obtain a supplement to the material from the permanent stations (see Tables 6—8). Scattered hydrographical material from the fjord complex, first and foremost collected by the Danish Biological Station, also exists from other years.

Table 5.

Salinity and temperature at St. III in the Inner Broad of the Isefjord off the Naval Station. Depths 6—7 m. 1941—1942.

		‰ S	°C	
13. 3.1941	0 m.	17.79	0.52 (from hole in ice)	
	5 m.	22.53	0.52	
28. 3.1941	0 m.	19.73	0.65	
	4 m.	19.83	0.17	
9. 4.1941	0 m.	20.77	4.2	
	5 m.	21.24	2.3	
25. 4.1941	0 m.	21.40	5.95	
	5 m.	21.40	5.80	
8. 5.1941	0 m.	21.29	7.3	
	5 m.	21.38	7.0	
29. 5.1941	0 m.	21.27	15.8	
	5 m.	21.24	14.3	
12. 6.1941	0 m.	21.26	14.74	
	5 m.	21.30	14.80	
25. 6.1941	0 m.	20.27	22.5	
	4 m.	20.46	22.0	
16. 7.1941	0 m.	20.12	22.4	
	4 m.	20.17	22.2	
30. 7.1941	0 m.	19.93	21.6	
	4 m.	19.92	21.2	
14. 8.1941	0 m.	19.60	17.1	
	4 m.	19.63	17.1	
27. 8.1941	0 m.	19.32	17.2	
	4 m.	19.32	17.2	
11. 9.1941	0 m.	18.94	15.5	
	4 m.	19.03	15.6	
30. 9.1941	0 m.	19.06	13.0	
	4 m.	19.08	13.0	
14.10.1941	0 m.	19.34	10.3	
	4 m.	19.36	10.3	
28.10.1941	0 m.	19.35	7.1	
	4 m.	19.35	6.8	
18.11.1941	0 m.	19.77	1.7	
	4 m.	23.88	3.2	
10.12.1941	0 m.	22.23	3.0	
	4 m.	22.23	3.0	
25. 3.1942	0 m.	..	1.3	(hole in ice)
	5 m.	..	0.9	
28. 4.1942	0 m.	20.34	7.7	
	5 m.	20.34	7.7	
19. 5.1942	0 m.	21.15	12.1	
	5 m.	21.18	12.0	
16. 6.1942	0 m.	20.97	14.4	
	5 m.	21.09	14.3	
21. 7.1942	0 m.	20.57	18.2	
	5 m.	20.57	18.2	
25. 8.1942	0 m.	20.23	19.1	
	5 m.	20.23	18.9	
29. 9.1942	0 m.	20.05	13.3	
	5 m.	20.07	13.3	

Table 6.

Salinity and temperature at St. I in the entrance to the Isefjord (lat. 55°53′7″ N., long. 11°49′4″ E.). Depth 9.5 m. Excursions in 1940.

		‰ S	°C
24. 6.1940	0 m.	16.40	19.20
	6 m.	18.95	19.45
1. 8.1940	0 m.	18.59	17.79
	6 m.	18.57	17.40
30. 8.1940	0 m.	22.03	14.59
	6 m.	22.01	14.60
15.10.1940	0 m.	21.82	10.8
	6 m.	24.07	11.5

Table 7.

Salinity and temperature at St. II in the Outer Broad of the Isefjord (lat. 55°53′7″ N., long. 11°49′4″ E.). Depth 9.5 m. Excursions in 1940.

		‰ S	°C
24. 6.1940	0 m.	19.14	20.21
	4 m.	19.45	19.60
	8 m.	20.21	17.83
1. 8.1940	0 m.	18.60	18.02
	4 m	18.68	17.70
	8 m.	18.77	17.59
30. 8.1940	0 m.	19.72	14.43
	8 m.	19.71	14.40
15.10.1940	0 m.	21.10	10.60
	6 m.	21.10	10.60

Table 8.

Salinity and temperature at St. III in the Inner Broad of the Isefjord off the Naval Station (lat. 55°43′ N., long. 11°49′ E.). Depth 7 m. Excursions in 1940.

		‰ S	°C
24. 6.1940	0 m.	20.66	21.10
	6 m.	20.68	20.30
1. 8.1940	0 m.	19.51	18.11
	4 m.	19.52	17.99
30. 8.1940	0 m.	19.29	14.40
	5 m.	19.29	14.39
15.10.1940	0 m.	20.74	10.5
	5 m.	20.73	10.5

Table 9.

29.10.1942. (Measurements made by Mr. Aage Jensen, Ph. D.).

		‰ S	°C
Tempelkrog (in the middle)	0 m	19.12	9.32
	2.5 m.....	21.05	9.02
Inner Broad (off the Naval Station)	0 m.....	20.52	9.42
	5 m.....	22.36	9.78

The salinity in the Outer and the Inner Broad is practically the same as at the entrance, if we consider the mean salinity of the year in question. Thus the mean salinity at Kyndby Havn for the year November 1st, 1942, to October 31st, 1943, was 19.5 ‰ (19.6 ‰ at Rørvig). As observations at the naval station in the Inner Broad for a couple of months are missing, the figure from here cannot be compared directly with the others, but the average salinity for the months of December—August, when complete observations from both Kyndby Havn and the naval station were available, in the former place was 19.7 ‰, in the latter place 20.2 ‰. Although the difference is slight, 0.5 ‰, the salinity seems to increase a little from Outer to Inner Broad. Similar results were obtained at the hydrographical sections made through the fjord at the excursions in 1940 and 1941 (see observations from the excursions on June 24th, 1940 and August 1st, 1940, Tables 7 and 8). The salinity in Tempelkrog is of fairly the same magnitude as in the Inner Broad (Table 9).

The above-mentioned salinities are only from the surface, but as the water-masses in the fjord generally are not stratified, this applies broadly speaking to the fjord water as a whole. Only after prolonged periods of calm weather the water-masses in the fjord can be distinctly stratified. This is e. g. the case of the Holbæk Fjord off the mouth of the Tuse Å, where the freshwater in such cases may settle above the salt water proper (see Petersen 1891). In calm weather minor differences may arise in the broads of the Isefjord between the salinities of the surface and those of the deeper layers of water. After a very long and calm period at the end of June 1940 (see Table 7) the salinity in the deeper layers of the Outer Broad was about 1 ‰ higher than the surface layers. In the Inner Broad, on the other hand, the salinity at the same time was the same in the surface layer and at the bottom (see Table 8). The only time when in the Inner Broad, outside times with melting of ice, there was an appreciable difference between the surface salinity and that at the bottom, was on November 18th, 1941 (see Table 5), the salinity at the bottom then being 4 ‰ higher than the surface salinity.

Although also the salinity in the entrance itself is generally the same from surface to bottom, there is in this place because of the connexion with the Kattegat an easy possibility of the formation of layers of different salinity. No prolonged period of calm weather is required for this. Thus we found there on October 15th, 1940, a distinct stratification (salinity at the surface 21.82 ‰, at a depth of 5 m. 24.07 ‰), whereas the water-masses in the fjord proper at that time was nowhere stabilized (see Tables 6—8).

The temperature in the shallow fjord is in summer higher than in the southern Kattegat. Table 4 shows the monthly means for 1942—43 at the surface at the various stations (daily measurements). The highest temperature for this period was found at the beginning of August (at Kyndby 21.8° C., at the naval station 21.6° C.). A still higher temperature was measured at the naval station on July 16th, 1941, viz. 22.4° C. Because of the easy conditions of mixing, the temperature, like the salinity, is as a rule the same from surface to bottom.

The Isefjord easily freezes over in winter. In the severe ice-winters 1939—1942 the fjord was on an average frozen over for 3 months, whereas it was practically ice-free in the winter of 1942—1943.

The current in the fjord is generally but slight. It is particularly due to the wind, but tidal currents also make themselves felt, particularly at the entrance to the fjord and in the channels on either side of Orø.

In the Isefjord the difference between the mean tide levels is nearly 20 cm., though higher at the vernal equinox.

At gales from the north (or particularly from the N. W.) great bodies of water are forced into the fjord. Under such conditions the current in the entrance may have a speed of up to $1^1/_2$ nautical miles, and also in sounds, e. g. on both sides of Orø, the current may be comparatively rapid. According to the Nautical-Meteorological Annual of 1929 a deviation of 1 m. from the ordinary height of the water is of common occurrence in the fjord, further the highest water hitherto known is at Hundested + 1.6 m., at Rørvig + 2.0 m., at Nykøbing + 1.8 m., at Orø + 2.0 m., and at Holbæk + 2.1 m.

Great bodies of water may likewise by gales from the south (or particularly from the S.E.) be blown out of the fjord, thus giving rise to extraordinary low water in the fjord. The lowest water known so far is at Hundested — 1.3 m., at Rørvig — 1.0 m., at Nykøbing — 1.2 m., at Orø — 1.6 m., and at Holbæk — 1.2 m.

Consequently great exchanges of water with the Kattegat take place during stormy weather. As gales from the N.W. are more frequent in Denmark than gales from the S.E., and as at the same time the salinity immediately outside the fjord is highest at gales from the N.W. because the south-going current in the Kattegat then is strongest in the Kattegat, the renewal of the water in the fjord from the outside generally takes place through water-masses which are somewhat more saline than appears from the mean salinity at the entrance.

It was shown on p. 8 that the lowest salinity of the year in the entrance to the fjord is found in July, whereas this already takes place in May in the southern part of the Kattegat. As regards the latter place, this is due to the fact that particularly great amounts of Baltic water at this time, in part because of the now prevalent eastern winds, flow out through the Sound. On the other hand, the salinity at the entrance of the fjord at gales from the east (particularly the southeast) will not be especially low as under such conditions water-masses flow out of the fjord.

At present it is impossible to make any definite statement as to the quantitative proportions of the exchange of water as regards the whole Isefjord area, but the exchange must at any rate be considered great. Only a single gale must mean a huge renewal of the water. A change in the height of the water of 1 m. at a depth of the water of at most 9 m. causes a comparatively enormous transportation of water out of or into the fjord. On the other hand, the freshwater supply is comparatively insignificant, thus not a single greatly water-bearing river debouches into the Isefjord. The area of precipitation from which water flows to the Isefjord (i. e. less the Roskilde Fjord) is only some 800 square km., not even three times the area of the fjord. Furthermore, this area of precipitation nearly exclusively consists of eutrophic areas (arable land and woodland), from which the greatest part of the precipitation by far will again evaporate (see further below, p. 16). Since, as mentioned above, the salinity in the Inner broad on an average is no lower than that of the Outer Broad, the supply of freshwater from the land + the rainfall must be supposed to be of fairly the same magnitude as the evaporation. It is difficult to offer any estimate of the evaporation. According to previous determinations by Colding and Westermann (see Ødum and Christensen, 1936) the evaporation from the lake Peblingesøen in Copenhagen is 130 per cent. of the precipitation, but as several conditions are somewhat different there from conditions in the Isefjord (e. g. the tem-

perature and protection from the wind) it is not possible with certainty to make any direct comparison. However, if we use the percentage mentioned above and put the area of the Inner Broad at 60 square km., evaporation—precipitation (put at 550 mm. a year) will be about 10 million cubic metres a year. The volume of water conveyed to the Inner Broad from the land in a year might therefore be estimated to be at most of this size, though presumably it is somewhat larger (estimated on the basis of the size of the area of precipitation). Thus there is reason to suppose that the salinity at the power station of Kyndby is either lower than that of the Outer Broad as whole, or that the water conveyed to the Inner Broad from the Outer Broad perhaps is slightly more saline than the water of the Inner Broad on an average, as the greater exchanges of water in the fjord preferably take place during gales from the northwest, when water from the Kattegat, the salinity of which is above the normal, is forced in through the entrance of the fjord (cf. p. 12).

C. Hydrography of the Roskilde Fjord.

The long and narrow Roskilde Fjord especially because of its form displays hydrographical conditions slightly different from those of the Isefjord proper. No particularly highly water-bearing rivers debouch into the Roskilde Fjord either, but as the area of precipitation is about 10 times that of the area of the fjord, the salinity decreases considerably towards the interior stretches of the fjord. According to Table 10 based on the Nautical-Meteorological Annual 1932 the mean salinity for the whole year (1895—1930) at Frederikssund (i. e. about half-way down the fjord, see the chart on p. 8) is 15.2 ‰. As mentioned above, the annual mean salinity at the entrance to the Isefjord is 19.4 ‰. The highest mean salinity at Frederikssund is reached in summer (June—July 16.3 ‰), the lowest in winter (December 14.6 ‰); see Table 10.

In the innermost part of the fjord daily measurements of the surface salinity have been made only for one year (Roskilde Harbour, November 1942—October 1943; see Table 3). For reasons to be discussed below the salinity in the Roskilde Fjord during this period was extraordinarily high, the mean at Frederikssund in the middle of the fjord November 1942—October 1943 being 17.3 ‰, at Roskilde 14.0 ‰. The highest monthly mean salinity at Roskilde was found in November (15.1 ‰), the lowest in Januar—March (monthly means 12.6 ‰). As we have only the figures for one year it is impossible to make a comparison with the means from 1895 to 1930 at Frederikssund as regards the times of occurrence of the maxima and minima of the salinity, the more so as the Frederikssund station during the period 1942—1943 only behaves completely normally as regards the occurrence of the maximum salinity (see Table 3).

Whereas thus the annual maximum

Table 10.

Mean salinities (‰ S.) and temperature (°C.) according to daily observations at the surface at Frederikssund 1895—1930 (according to the Nautical-Meteorological Annual 1932)

	‰ S	°C
January	14.7	0.6
February	14.7	0.5
March	14.7	1.9
April	14.7	6.0
May	15.3	11.9
June	16.3	16.4
July	16.3	18.3
August	16.1	17.3
September	15.5	13.9
October	14.8	9.2
November	14.8	4.7
December	14.6	1.7
Year	15.2	8.5

salinity in the Roskilde Fjord (Frederikssund) is reached in the summer (June—July) and the minimum in the middle of the winter (December), conditions in the entrance to the Isefjord, as mentioned above, are exactly the opposite, the maximum here being reached in February and the minimum in July.

Conditions of temperature in the Roskilde Fjord are identical with those in the broads of the Isefjord, thus the highest temperature in 1943 at Roskilde was recorded at the beginning of August (21.9° C.; see further Table 4).

Normally the water-masses in the Roskilde Fjord are mixed from bottom to surface as in the Isefjord. In calm periods, however, a temperature stratification may also be established here, and as at the same time the current at the surface and at the bottom will often be somewhat different in the fjord, sometimes in opposite directions, there may also be differences between the salinities of the surface and the bottom layers. Thus a northerly current of 14 cm./sec. according to unpublished investigations made by Dr. I. P. Jacobsen in September 1913 was measured at a station immediately north of the bridge at Frederikssund at a depth of 1 and 2 m., while a northerly current of 8 cm./sec. was measured at a depth of 6 and 7 m. The salinity in this case was 15.8 $^0/_{00}$ at the surface and 16.3 $^0/_{00}$ at the bottom.

Ebb and flow in the Roskilde Fjord correspond to conditions in the Isefjord. The tidal current in the southern part of the Roskilde Fjord is insignificant, but in the northern part it flows with rather a considerable speed. This is particularly the case in the narrow Kulhus Rende. Here an outgoing current of 44 cm./sec. (= about $^3/_4$ knot) was measured during quite a calm period on September 8th, 1913 (Dr. I. P. Jacobsen). At the time of the measurement, the wind was soft both in the place and at the neighbouring meteorological stations (the force of the wind was about 1 Beaufort), and in the preceding days the weather was calm, too. Thus there was no stowage of water conditioned by wind which during the measurements might be under equalization. Under conditions when there is a stowage of water in the fjord, the current in Kulhus Rende may be of considerably greater force than $^3/_4$ knot. In this connexion it may be mentioned that according to the Nautical-Meteorological Annual 1929 deviations of 0.6 m. from the normal height of the water are common. The lowest water hitherto recorded from Roskilde is —1.1 m. and the highest water +1.7 m.

D. On Changes in the Salinity of the Roskilde Fjord.

Since 1895 the Meteorological Institute has made daily measurements of temperature and salinity in the Roskilde Fjord at Frederikssund. The material is published every year together with similar material from a long series of other stations in the Danish waters in the Nautical-Meteorological Annual (Nautisk-Meteorologisk Årbog). Means for the whole material down to 1930 are also published in the annual for 1932.

It appeared that the salinity in the Roskilde Fjord during the years in which I made my investigations was rather different from the normal. A brief account of this will be given in what follows, as also possible causes of the change will be discussed in connexion with the quantitative aspects of the exchange of water in the fjord.

The mean salinity at Frederikssund 1895—1930 is 15.2 $^0/_{00}$, in the period 1895—1938 an annual mean salinity of 17.1 $^0/_{00}$ or more was never observed. Furthermore, an annual mean salinity of 16.1—17.0 $^0/_{00}$ was observed only 5 times during this 44-year period.

In the period 1939—1942, on the other hand, the mean salinity was 18.5 $^0/_{00}$, the lowest

annual mean salinity being 17.9 ‰. The annual mean salinities for this period are listed below, the following years, 1943—1946, being included, too:

1939	17.9 ‰ S.
1940	19.1 ‰ S.
1941	18.8 ‰ S.
1942	18.3 ‰ S.
1943	17.1 ‰ S.
1944	16.6 ‰ S.
1945	16.7 ‰ S.
1946	15.9 ‰ S.

The Roskilde Fjord receives salt water from the northernmost part of the Isefjord and freshwater through precipitation and supply from the land. Furthermore evaporation plays a part. This is of fairly the same order of magnitude as the precipitation and has the opposite effect to the latter.

Supply of freshwater = precipitation + supply from the land — evaporation. Changes in the salinity of the Roskilde Fjord may be due either to qualitative or to quantitative changes in the supply of salt water or to quantitative changes in the supply of freshwater.

As to inflowing salt water, the salinity in the area of the entrance to the Isefjord in 1939—1943 was 19.5 ‰, while the mean salinity 1895—1930 for this area is 19.4 ‰. All figures originate from the Nautical-Meteorological Annual. Thus no qualitative change of the inflowing salt water at all seems to have taken place. As regards quantitative changes of this inflowing water there is no information at all available.

In 1933 the grass-wrack (*Zostera marina*) disappeared nearly completely from the Isefjord area because of an epidemic disease. Before 1933 large amounts of in part very long-leaved grass-wrack were growing in the fairly shallow water. At any rate it must have impeded the current somewhat. There is, therefore, a possibility that the exchange with the more salt water-masses outside the Roskilde Fjord increased from 1933 on. The mean salinity at Frederikssund 1933—1938, however, was 15.6 ‰, i. e. quite normal. Not until a period beginning in 1939 did the high increase in salinity set in. As this even happened at a period when the grass-wrack was returning—in 1943 the growths of this plant were again very large, in part of nearly the same size as before 1933—the grass-wrack can probably completely be left out of consideration as a cause of the increase in salinity.

The supply of freshwater to the fjord is still left to be considered. The evaporation has not been examined at all, but the rainfall is known as the Meteorological Institute makes measurements of this at some stations in the area of precipitation of the Roskilde Fjord. On the basis of the material published in the meteorological annuals I have calculated the annual mean rainfall for the whole area of precipitation of the Roskilde Fjord in the period 1900—1942. As boundaries the water-sheds above ground have been used, which correspond fairly to the water-sheds for the subsoil-water, as I have been able to observe it by a comparison with the observation material in the Well-boring Archives of Denmark's Geological Investigations. Afterwards it was investigated whether the rainfall has any influence on the salinity in the Roskilde Fjord. This was done through correlation calculations.

If we correlate the rainfall in the individual year with the salinity, it appears that the rainfall has a considerable influence on the salinity. However, the water-masses in the Roskilde

Fjord are by no means exchanged completely every year. About half of the volume of water is stationary from one year to the next. Provisionally I shall not go into the calculation of this quantity, which involves considerable possibilities of error, but only show the partial staying of the water-masses in the fjord from year to year by giving the correlation between the salinity of each year and that of the preceding year in the period 1900—1943. It is $+0.61 \pm 0.10$.[1]

Thus it is a case of a considerable positive correlation, which can only mean that an essential part of the volume of water of the fjord is stationary from one year to the following year. This is not due to positive correlation between the rainfall of each year and the following year, as this in the period 1912—1942 was $+0.16 \pm 0.17$.

In order to eliminate the influence of the salinity of the previous years on that of the individual year I have not at the calculations of the correlation between rainfall and salinity used the salinity itself, but the difference between the salinity of each year and that of the preceding year. The period used was the years 1900—1936 (37). The greatest correlation (-0.68 ± 0.09) was obtained by shifting the "salinity" by 4 months forwards in relation to the rainfall. The rainfall in the area of precipitation of the Roskilde Fjord clearly influences the salinity in the fjord.

As furthermore, as shown above, there is a considerable positive correlation between the salinity of each year and that of the following year, we shall, particularly in periods with several years with deviating conditions of precipitation, find considerable deviations with regard to the salinity in the fjord.

The average annual rainfall in the whole area of precipitation of the Roskilde Fjord for the period 1900—1942 is 564 mm. In the 4-year period 1938—1941 it was only 478 mm. In no other 4-year period in this century the rainfall has been only approximately so low. The period coming closest to it is 1906—1909 with an annual mean precipitation of 522 mm. The period 1938—1941 was even preceded by two years with a rainfall below the mean, viz. 540 and 553, respectively. Therefore we can very well understand that the salinity during the years 1939—1942 was particularly high.

The salinity in the following year (1943) was also high: 17.1 $^0/_{00}$. This is, however, a conspicuous reduction in relation to the salinity of the preceding year, which is also in accordance with the fact that the rainfall in 1942 was not particularly low: 566 mm. Finally the mean salinity in 1944—1946 dropped to 15.9 $^0/_{00}$. When the salinity in the Roskilde Fjord has been very high, some time will pass before it drops to the normal again, as a considerable part of the water in the fjord is stationary from one year to the other.

The area of the Roskilde Fjord is 117 square km., while its area of precipitation is about 1000 square km., which must mean that the greater part of the freshwater conveyed to the fjord has fallen on areas of land. It is rather difficult to form a definite opinion on the question how great a part of the precipitation of the area of precipitation of the Roskilde Fjord will flow into the fjord. According to the hydrometrical measurements of the Heath Society the average flow-off through the river Havelse Å (tributary country 67 square km.) is 4.9 l/sec. per square km., and through Værebro Å (tributary country 143 square km.) 3.4 l/sec. These are the only two streams from the area which have been examined, and, as appears from the

[1] Here, as in all the following calculations, this formula was used:

$$r = \frac{\Sigma ab - \frac{\Sigma a \cdot \Sigma b}{n}}{\sqrt{\left(\Sigma a^2 - \frac{(\Sigma a)^2}{n}\right)\left(\Sigma b^2 - \frac{(\Sigma b)^2}{n}\right)}}.$$

above, they give an average flow-off of respectively 28 per cent. and 19 per cent. of the rainfall of the tributary country. Assuming that 25 per cent. of the rainfall of the whole tributary country of the fjord reaches the fjord, this means that about 140 million tons of freshwater is supplied every year from the land. The precipitation over the fjord itself (on an average 66 million tons a year) is of the same order of magnitude as the evaporation (cf. COLLIN's investigations from the lake Peblingesøen in Copenhagen, of which an account is given in ØDUM and CHRISTENSEN, 1936). In relation to the supply of freshwater to the fjord these quantities at any rate will be without importance as their effects on the whole will cancel out.

The municipality of Copenhagen has for many years pumped water in the areas drained off into the Roskilde Fjord. A new, particularly great pumping was started at Lejre in 1937. Since then 12 million tons of water have been pumped here every year. To all appearance they would otherwise have flowed into the fjord, whereas now they will finally flow into the Sound instead. Thus about 9 per cent. of the total average supply of freshwater from the land after 1937 will no more reach the fjord, a fact which of course must be of some importance for the salinity in the fjord.

To illustrate how great this importance has been it is necessary to know the quantitative conditions at the exchange of water of the fjord. As this is not properly the case, conditions will be illustrated by an ideal example instead. We shall imagine a container of 440 million cubic m. (the volume of the Roskilde Fjord). Every year 140 million cubic m. freshwater and a quantity of salt water with a salinity of 19.4 $^0/_{00}$, which corresponds to the salinity at the entrance to the Isefjord are poured into this container. There is no evaporation from the container and a complete mixing of the volumes of water takes place. Hence an annual amount of 647 million cubic m. water with a salinity of 15.2 $^0/_{00}$ leaves the container by overflowing.[1]

A calculation of the salinity of the water overflowing from the container, if 12 million cubic m. freshwater less is poured into the container every year, conditions otherwise being the same, gives the values 15.5 $^0/_{00}$ S.[2] Under these conditions the salinity of the outflowing water thus would have increased but insignificantly, even though the supply of freshwater was decreased by about 9 per cent. The increase in salinity in the Roskilde Fjord because of the pumping at Lejre must presumably be of the same order of magnitude. If conditions in the fjord were otherwise constant, the mean salinity thus would have increased from 15.2 $^0/_{00}$ to about 15.5 $^0/_{00}$.

If in the ideal example the salinity of the outflowing water were to increase to 18.5 $^0/_{00}$ by only the amount of freshwater added being changed, this can be calculated to be 25 million cubic m.[3] Thus the supply of freshwater is only 18 per cent. of the original supply.

[1] With x being the amount of inflowing 19.4 $^0/_{00}$ salt water and y the amount of outflowing 15.2 $^0/_{00}$ salt water, we get:

$$140 + x = y$$
$$x \cdot 19.4 = y \cdot 15.2$$
$$x = 507 \text{ and } y = 647.$$

[2] With z = the salinity in the now outflowing water, we get:

$$507 \cdot 19.4 = 635 \cdot z$$
$$z = 15.5.$$

[3] With v = the amount of inflowing freshwater and u = the amount of outflowing water, we get:

$$v \cdot 507 = u$$
$$507 \cdot 19.4 = u \cdot 18.5$$
$$v = 25$$
$$u = 532.$$

Was the supply of freshwater to the Roskilde Fjord similarly in the period with the high salinities only 18 per cent. of the normal? In the period 1938—1941 the rainfall was 15 per cent. below the mean. The amount of the outflow above ground and underground thus in such a period becomes considerably smaller than 15 per cent. below the mean, as it is conditioned by the surplus between rainfall and evaporation. Possibly a reduction of 82 per cent., as it was to be if there were a complete agreement with the ideal example, is somewhat too great. First of all this would be due to the fact that the result of the increase in salinity at Frederikssund is somewhat higher than that of the water-masses of the Roskilde Fjord as a whole, for a minor displacement of the isohalines towards the head of the fjord without the average salinity of the fjord being particularly changed, must also give rise to an increase in the salinity at Frederikssund, the more so as this town is situated in a place where the isohalines generally are found very close together. In a period with a smaller supply of freshwater to the fjord we must reckon with a relative advance of the salt water.

Therefore, to estimate the increase in salinity in the fjord, a station situated farther into the fjord would have been more useful. To judge this question we must, however, content ourselves with daily measurements off the harbour of Roskilde at the head of the fjord, which were made through a single year, November 1942—October 1943, combined with more accidental measurements made in the course of time in this place.

In the period just mentioned the mean salinity was 14 $^{0}/_{00}$, while the total material from the time before 1938 gives a salinity of about 12 $^{0}/_{00}$. In the period November 1942—October 1943 the mean salinity at Frederikssund was about 17.3 $^{0}/_{00}$. The increase in salinity at Frederikssund and at Roskilde thus seems to have been of fairly the same size, at any rate not much smaller at the head of the fjord. Significant changes in the various diagrams used in this paper thus presumably would not have appeared if it had been possible to give exact values for the salinity of the water-masses in the fjord. Minor corrections, however, would no doubt make their appearance, thus as regards the decrease in the supply of freshwater from the land which took place in 1938—1941.

According to what is stated on p. 17, the Roskilde Fjord every year receives a supply of 507 million cubic m. seawater (19.4 $^{0}/_{00}$ S.) and 140 million cubic m. freshwater. These water-masses are mixed with the masses present, i. e. 440 million cubic m. If the water-masses intermixed completely, we should therefore consider that 41 per cent. of the water-masses were stationary in the fjord from year to year. Although we cannot of course take it for granted that the mixture is very complete, the order of magnitude of the body of water which is stationary from year to year is presumably correct, which agrees with the considerable positive value for the correlation between the salinity of every year and that of the following year at Frederikssund. As stated above, this correlation is + 0.61.

E. Oxygen, Hydrogen Ion Concentration, and Nutrient Salts.

In such a shallow fjord as the Isefjord the wind will generally prevent any effective stabilization of the water-masses for a prolonged time. The water-masses therefore will as a rule be fairly in equilibrium with the oxygen of the atmosphere. There are exceptions, partly in winter, when the ice covers the fjord, partly in summer during prolonged warm and calm periods.

At the end of the ice period 1941—1942 (25.3.1942) there was in the Inner Broad at a depth of 5 m. an oxygen saturation of 71 per cent. Thus there was apparently no great loss

of oxygen. At low temperatures the consumption of oxygen by bacteria and animals is slight. However, an essential cause of the relatively high percentage of oxygen is presumably the phytoplankton, the spring production of which had already begun under the ice. Probably a considerable amount of oxygen had been produced by the photosynthesis of the plankton algae. In places where there had been pollution by outflow of sewage water or the like we should expect more or less complete oxygen-exhaustion also at the end of the ice period.

Table 11.

24.6.1940.

Depth in metres	Outer Broad		Inner Broad	
	t	O_2 %	t	O_2 %
0	20.2	100	21.1	97
4	19.6	100	..	..
6	..	..	20.3	78
8	17.8	66	..	..

At the end of June 1940, after a long warm and calm period an excursion was made through the fjord. Table 11 shows conditions of oxygen and temperature at a station in the middle of the Outer Broad and at a station in the Inner Broad.

In the deep in both places a distinct undersaturation of oxygen thus was found, which, however, will be equalized as soon as the volumes because of the wind are mixed. One month later (1.8.1940) there was thus at the station in the Outer Broad at a depth of 8 m. a percentage of oxygen of 92 and at the station in the Inner Broad at the bottom of 93. A relative minimum of oxygen in the deeper layers of water may be established in a comparatively short time, particularly because of exchange with the bottom. The Winkler method was used at the determinations of the oxygen.

Table 12.

Phosphate in the Inner Broad off the Naval Station (St. III). Depths 6—7 m. 1940 and 1941 (until the middle of August).

		mg. $P\text{-}P_2O_5/m^3$
24. 6.1940	surface	5
	depth of 6 m.	15
1. 8.1940	surface	3
	depth of 4 m.	5
30. 8.1940	surface	0
	depth of 5 m.	0
15.10.1940	surface	0
	depth of 5 m.	0
13. 3.1941	surface	20
	depth of 5 m.	15
28. 3.1941	surface	15
	depth of 4 m.	12
9. 4.1941	surface	0
	depth of 5 m.	0
25. 4.1941	surface	0
	depth of 5 m.	0
29. 5.1941	surface	2
	depth of 5 m.	1
12. 6.1941	surface	13
	depth of 5 m.	20
25. 6.1941	surface	3
	depth of 4 m.	5
30. 7.1941	surface	15
	depth of 4 m.	15
14. 8.1941	surface	8
	depth of 4 m.	8

pH was determined repeatedly in samples of water from the Inner Broad. As might be expected pH is always about 8.2 both at the surface and at the bottom. Conditions at the naval station on June 16th, 1942, may serve as an example, pH here at the surface being 8.23 and at a depth of 4 m. 8.22. pH was determined photometrically (double-wedge photometer) with creosol red as indicator and with consideration to correction for salt.

The nutrient salts play an extremely important part for our understanding of at any rate the quantitative aspect of the plant production. The salts containing nitrogen and phosphorus are here of primary importance, the other substances necessary for the plants generally being present in sufficient quantities in seawater. For diatoms, however, the content of silicium also plays a role.

In the years 1940—1942 a fairly considerable number of determinations of the nutrient salts were made in the Isefjord. These were generally made by Mr. F. Hermann, M. Sc., either in the place in question or in the Hydrographical Laboratory (of the Commission for Fishery and Sea Investigations of Denmark). For some periods the determinations, however, were made by the author.

Table 13.

Nutrient salts in the Inner Broad off the Naval Station (St. III). Depths 6—7 m. From the end of August 1941 to the end of September 1942.

		mg. $P\text{-}P_2O_5/m^3$	mg. $N\text{-}NO_3/m^3$	mg. $N\text{-}NO_2/m^3$	mg. $N\text{-}NH_4/m^3$
27. 8.1941	surface	2	..	0	25
	depth of 4 m.	2	..	0	15
11. 9.1941	surface	0	7	0	200
	depth of 4 m.	0	..	0	200
30. 9.1941	surface	1	..	..	..
	depth of 4 m.	1	..	..	..
14.10.1941	surface	2	0	0	150
	depth of 4 m.	2	0	0	150
28.10.1941	surface	2	0	1	175
	depth of 4 m.	2	0	2	..
18.11.1941	surface	4	30	2	200
	depth of 4 m.	5	50	2	450
10.12.1941	surface	1	..	4	300?
	depth of 4 m.	1	..	4	..
25. 3.1942	surface	9	150	9	350
	depth of 5 m.	20	180	18	300
28. 4.1942	surface	1	240	7	100
	depth of 5 m.	1	240	9	250
19. 5.1942	surface	1	20	0	100
	depth of 5 m.	1	20	1	200
16. 6.1942	surface	4	20	0	350
	depth of 5 m.	4	20	0	240
21. 7.1942	surface	1	4	0	50
	depth of 5 m.	1	6	1	100
25. 8.1942	surface	7	20	0	ca. 25
	depth of 5 m.	9	60	1	ca. 25
29. 9.1942	surface	7	25	0	ca. 10
	depth of 5 m.	7	30	0	ca. 10

On the excursions through the fjord in 1940 only phosphate was determined. The same was the case in the former half of 1941 at the investigations twice a week in the Inner Broad off the naval station. In the latter part of 1941 and in 1942 besides phosphate also nitrate, nitrite, ammonia, and silicate were determined in this place. The determinations of silicate will not, however, be published as they are in part rather defective. At the determinations of the nutrient salts Wattenberg 1937 was followed, at the determination of nitrate the strychnine method and at the determination of ammonia the precipitation method were used.

The results are listed in Tables 12—15 (see further figs. 17—20).

A detailed discussion of the question of nutrient salts will be found in connexion with the question of production of matter by the phytoplankton, p. 37, as these two factors are

closely connected. It should only be noted here that in all seasons we generally in the Isefjord find somewhat greater quantities of the nutrient salts than in the surface layer of the Kattegat. However, it should not be forgotten that the free quantities of nutrient salts are not of primary

Table 14.

Phosphate in the entrance area (St. I). Depth 7.5 m. 1940.

		mg. $P\text{-}P_2O_5/m^3$
24. 6.1940	surface	5
	depth of 6 m.	7
1. 8.1940	surface	3
	depth of 6 m.	3
30. 8.1940	surface	0
	depth of 6 m.	0
15.10.1940	surface	5
	depth of 6 m.	0

Table 15.

Phosphate in the Outer Broad (St. II). Depth 9.5 m. 1940.

		mg. $P\text{-}P_2O_5/m^3$
24. 6.1940	surface	3
	depth of 4 m.	0
	depth of 8 m.	15
1. 8.1940	surface	3
	depth of 4 m.	5
30. 8.1940	surface	0
	depth of 7 m.	2
15.10.1940	surface	0
	depth of 6 m.	0

interest. Indeed, these are only the surplus. The quantity which is first and foremost of interest is the annual consumption of nutrient salts, which can only be determined indirectly and very roughly.

Considerable amounts of ammonia are sometimes found in the fjord, both in summer and winter (see fig. 13). The reason for this will be discussed on p. 39.

F. Conditions of Light in the Fjord.

The light in the various layers of water primarily depends partly on the light falling on the surface, partly on the transparency of the water; but also other factors assert themselves, such as the direction with which the rays of light strike the surface, and the consistence of the latter, as e. g. a wind-swept surface of the sea because of the contents of air bladders will both absorb and reflect greater quantities of light than a calm surface.

No investigations of the quantity of light striking the surface of the water in the Isefjord were made. We must content ourselves with the measurements made in Copenhagen continuously for about two years (Romose 1940). Conditions in the Isefjord area in 1940—1943 presumably more or less corresponded to these. It would be very desirable if continuous measurements of light would be made at various meteorological stations in Denmark. At the present stage of technics such measurements are neither difficult nor particularly expensive.

Measurements of the decrease in light with the depth were made in the Isefjord in 1940—1941. These measurements were chiefly made at the permanent station in the Inner Broad off the naval station in 1941, but also on the excursions through the whole fjord in 1940.

The measurements were made with the aid of a submarine photometer constructed by Conservator Nielsen (of Danmarks tekniske Højskole) on the basis of a design by the present writer (see fig. 2). The photometer has been in use since 1935. In principle it is like other modern photo-electrical submarine photometers, but as it has proved to be quick and easy to handle in practice, a detailed description of it will be given here.

Three big (diameter of surface sensitive to light: 58 mm.) photo-cells (system Photron,

Bercowitz und Sohn, Berlin) are placed each in its watertight container. The cells used are of a robust type, and as at the same time the measurements are used only relatively and the resistance of the measuring instrument is very low (see below), no corrections are necessary. Checking partly by means of a photometer adjusted thermo-electrically and partly by means of filters of neutral glass has practically shown proportionality between light-intensity and current read within the areas of measurement used. A Wratten filter no. 48a (blue) and the Schott filters (Schott und Gen. Jena) GG 11.2 mm. (green) and RG 2.2 mm. (red), respectively, were placed above the photocells. The upper side of the container is made of thick glass matted inwards. Furthermore, discs of frosted glass are placed above the windows proper, by which means we succeed in keeping the light reaching the photocell within the limits of proportionality between light-intensity and current. Tubes with calcium chloride are placed in all containers in order to prevent the glasses from getting misted when the measurements are made in cold water.

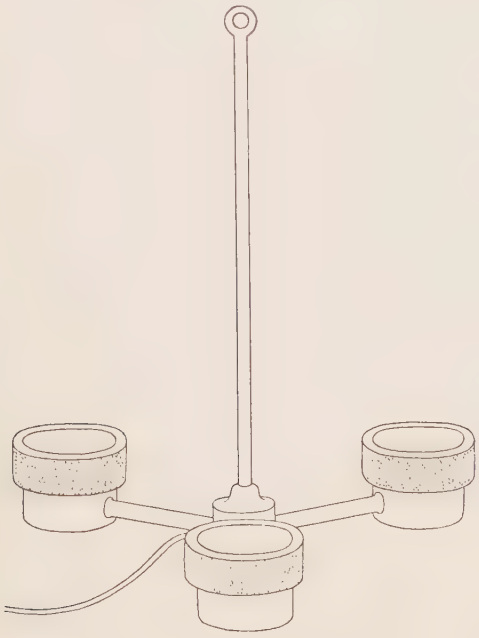


Fig. 2. The submarine photometer.

The above-mentioned containers are connected with a central container from which starts the cable leading to the measuring instrument above the water. In connexion with this central container is a rod at the end of which the wire from which the photometer is hanging is placed. In the cable there are four wires, one which is common to all photocells and further one to each of the three cells. By means of a simple device the various cells may in turn be connected with the measuring instrument, a doubly suspended micro-ammeter with a resistance of 100 ohm for all ranges (also supplied by Bercowitz und Sohn). For the checking of the light striking the surface of the water a fourth photocell was placed above the water (and connected with the same measuring instrument). Immediately before each measurement with the submarine photocells the intensity of the light above the water was recorded. The photocell above the water was exclusively used to correct for the measurements made with the submarine cells if the light-intensity varied during the measurement.

The wire (in small boats a log line) connected with the photometer passes over a wheel placed at the end of a long beam (or rod in a small boat). In sunshine care must be taken that the ship or boat is stationed in such a way that the photometer cannot get into a shadow.

All measurements are relative. After correction of the measurements on the basis of the measurements above the water the "absorption coefficient" k_s was calculated on the basis of the equation $\frac{I}{I_0} = e^{-k_s \cdot L}$, L being the thickness of layer of water in m., in which the intensity of light is reduced from I_0 to I, and e being the basic figure for the natural logarithms. What is measured is not what in physics is generally understood as the absorption coefficient, as, in order that the equation $\frac{I}{I_0} = e^{-k \cdot L}$ may be used, it is required that the rays of light have a vertical direction in relation to the surfaces where the light-intensities I and I_0 are measured. However, this is only the case when the sun is in the zenith.

If the angle (A) at which the rays of light in the water meet the vertical is known, the following formula may be used:

$$\frac{I}{I_0} = e^{-k \cdot \frac{L}{\cos A}}.$$

As will be shown below, the angle A can only be determined immediately below the surface and in sunshine. Farther down the light is diffused more or less by the plankton organisms, particles and molecules. Therefore it is not possible to calculate the correct absorption coefficient. The same is also the case in dull weather immediately below the surface. As the biologically essential thing is the reduction of the light from depth to depth the formula $\frac{I}{I_0} = e^{-k_s \cdot L}$ ought to be used, as the absorption coefficient k_s means the "adapted submarine absorption coefficient".

The decrease of the light intensity downwards into the layers of water is due to absorption and reflection, partly from the water molecules, partly from the dissolved substances, partly from the suspended substances (inorganic and organic), and finally from the plankton organisms. Dissolved substances ("yellow substance", presumably humus compounds; see KALLE 1938) are of some importance as regards differences in the penetration of light into the water in the various areas. Suspended particles originating from the bottom and plankton organisms in this respect, however, are of much greater importance. Suspended particles are of any appreciable importance only near the shore. In the Isefjord, where the depths are small and where, moreover, the bottom is soft, the deposited particles may be of exceedingly great importance for the transparency of the water. In rough weather it is not necessary for the ascertainment of this to make measurements of light in the inner parts of the fjord complex. The water is muddy to look at, and if a sample of water is left for sedimentation, a layer of particles will soon collect on the bottom.

In really stormy weather no measurements of light were made in the Isefjord as the small boats at our disposal for the investigations (a rowing boat at the permanent station in the Inner Broad) did not admit of work under such conditions. Particularly measurements of light are rendered difficult, as it is not possible to keep the photometer at a definite depth.

The lower the depth is, and the finer the kind of bottom deposits, the more easily can the bottom material be stirred up. The Holbæk Fjord is thus greatly exposed to having bottom material suspended in the water, the depth outside the shoals here being only about 5 m., and further the bottom consists of quite soft mud. Moreover, the fjord is open to westerly and easterly winds.

In the first report from the Danish Biological Station C. G. JOH. PETERSEN in 1891 took a survey of the Holbæk Fjord, which was the object of investigations during the first working year. Here PETERSEN also discussed the conditions of transparency of the fjord water, recording the depths at which a white ball disappeared from sight. The transparency varied between 2 and 12 feet, and as a rule was 6—8 feet. PETERSEN's views of the causes of conditions of transparency, with a single exception (on which see below), more or less correspond to those advanced in the present paper.

In the Inner Broad the water-masses generally did not get so "muddy" as in the Holbæk Fjord. The greater depth, about 7 m., is no doubt the primary cause. Near the shore there is, however, some difference. In the west, where the shallow water extends far out, the bottom is generally a little mixed with clay or mud, whereas in the east the bottom contains practically no mud or clay. At an on-shore wind the water-masses therefore are least transparent in the west.

In the Outer Broad with the somewhat greater depth (about 9 m.) and the somewhat firmer bottom deposit, the stirring up of matter from the bottom in rough weather is far from being of so great importance as in the Inner Broad.

In the entrance to the Isefjord the bottom is pure sand. Normally there will therefore be no appreciable stirring up of bottom material. During a strong gale, however, the sand will be suspended in the volumes of water, partly because of the exposure of the place (open towards the Kattegat), and partly because of the small depths on the threshold in the entrance. Under such conditions, however, no measurements of light were made.

The large amount of plankton has been mentioned as the second particularly important cause of the reduction of the transparency of the water. It is of course the phytoplankton which is of special importance. Therefore the season plays an important role. As we shall see below, this plankton is very scanty in the darkest time. In this season the water is therefore clear in calm periods. The same is the case in other seasons when the phytoplankton for some reason or other is slightly developed. At the discussion of the photometrical material this will be shown in detail. PETERSEN 1891, p. 164, mentions that the water in the Holbæk Fjord after a gale is cleared sooner in winter than in the spring. It was not possible for PETERSEN to offer any reasonable explanation of this fact. The occurrence of so enormous amounts of phytoplankton as are actually present was unknown at the time. Now we can understand that in times with much plankton the water does not become really clear again after a gale.

Table 16.

Measurements of Light in the Inner Broad off the Naval Station (Depth 5 m.).

Date	Time	Weather conditions	k_s (1—4 m)			Light at a depth of 4 m in percentages of light immediately below the surface		
			blue	green	red	blue	green	red
24. 6.1940	16.20	Bright	0.622	0.236	0.547	8.2	38.9	11.9
1. 8.1940	16.30	Bright	0.840	0.400	0.675	3.4	20.2	6.8
30. 8.1940	16.00	Bright, slight swell. Wind force 5	0.899	0.596	0.896	2.7	9.3	2.8
15.10.1940	15.50	Dull	0.977	0.543	0.752	2.0	11.9	4.9
29. 5.1941	18.30	Bright, light easterly wind	0.925	0.480	0.742	2.6	15.0	5.1
12. 6.1941	19.00	Slightly clouded, strong wind from the northwest	0.718	0.467	0.544	5.6	15.5	11.5
25. 6.1941	19.00	Bright, calm	0.450	0.170	0.512	19.5	50.8	12.9
16. 7.1941	18.30	Slightly clouded, calm	0.600	0.347	0.651	9.1	25.0	7.4
30. 7.1941	19.30	Bright, calm	0.818	0.404	0.570	3.9	20.0	10.2
14. 8.1941	18.30	Dull, nearly calm	1.450	0.754	0.964	0.6	4.9	2.1
27. 8.1941	18.30	Dull, rather strong wind from the west	0.945	0.605	0.753	2.3	8.9	4.9
11. 9.1941	19.00	Much overcast, wind insignificant	0.805	0.529	0.693	4.0	12.2	6.3
30. 9.1941	13.00	Bright, breeze from the southeast, heavy sea	1.140	0.632	0.805	1.0	8.0	4.0
14.10.1941	13.00	Dull, light wind from the west	0.276	0.325	0.482	33.1	27.2	14.6
28.10.1941	13.00	Cloudy, nearly calm	0.528	0.337	0.528	12.2	26.0	12.2
18.11.1941	13.00	Foggy, calm	0.393	0.285	0.581	20.8	32.0	9.8
10.12.1941	13.00	Slightly clouded, calm	0.250	0.223	0.302	36.8	41.1	29.9

As for the Inner Broad there is a fairly copious material on the penetration of light, as besides on the excursions in 1940 measurements of light were also made in the period May—December 1941 about twice a month at the permanent station off the naval station Bramsnæsvig. All observations from there are collected in Table 16.

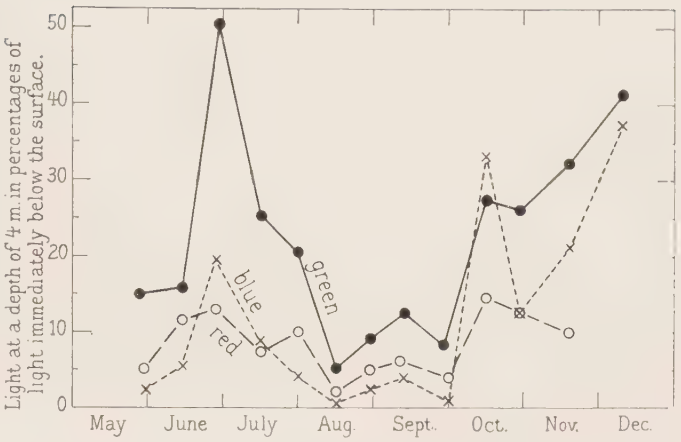


Fig. 3. Light at a depth of 4 m. off the naval station, Bramsnæsvig.

The depth was 5 m. Measurements of light were made down to a depth of 4 m. Besides the submarine absorption coefficients for the light colours blue, green, and red it is stated how many per cent. of light in relation to the light immediately below the surface were detected at a depth of 4 m., the three light colours being given separately.

In fig. 3 it is further shown in graphic representation how conditions of light varied in the period May—December 1941. It appears from the curves of this figure as well as from Table 16 that the transparency varied greatly during this period. Likewise the relative proportion between the transparency for the various light colours also varied.

With the exception of October 14th, 1941, the green rays penetrated best. On that day the blue rays penetrated slightly better than the green. If the water was comparatively transparent the blue rays penetrated better into the water than the red rays, whereas the red rays penetrated better into the water than the blue rays in periods with highly turbid water.

As mentioned above, it is primarily the content of plankton algae and of suspended particles from the bottom that causes the penetration of the rays of light into the water-masses to be reduced. The measurements of light were generally made under calm weather conditions, never in stormy periods. It thus appears that it is the amount of plankton which primarily conditions the reduction of the power of penetration when investigations were made. On the days when weather conditions were somewhat unsettled, it can also be shown that suspension in the water of bottom material was of some importance, at any rate, for the penetration of light.

It appears from the curves in fig. 3 that the light at the end of May penetrated relatively badly into the water-masses. This is in accordance with the fact that at that time a rich phytoplankton was found in the Inner Broad (cf. e. g. the curve in fig. 21, p. 45). Then in June the water became comparatively transparent (observations on June 12th, however, are greatly influenced by the weather conditions; see below). This is in accordance with the fact that in June there was a marked minimum for the phytoplankton. In July, August, and September there was another high maximum for the phytoplankton, with the absolute maximum in August. This is in perfect agreement with conditions of the penetration of light as the light then penetrated very badly into the water-masses.

In October and November the amount of plankton was greatly reduced, to reach a minimum in December. Correspondingly the transparency of the water increased highly in this period. On December 10th the intensity for the green light thus was reduced to only 41

per cent. in the uppermost 4 m. Also the blue light had a considerable power of penetration: in the uppermost 4 m. the blue light was reduced to 37 per cent.

Already under somewhat unsettled weather conditions it was possible to observe the influence of these upon the transparency of the water. Thus, to judge from the plankton, we should have expected a considerably greater transparency than the one shown on June 12th, 1941 (see Table 16). To all appearance this was due to the unsettled weather conditions on that day. The same was the case on September 30th, 1941. In such a shallow area with a soft bottom even moderately unsettled conditions will cause material from the bottom to be suspended in the water. Even though no measurements of light were made under stormy conditions, it should be mentioned that on a stormy day at the end of March 1941 the volumes of water in the Inner Broad were so turbid that actually a layer of mud settled on the bottom when a sample of water was left to stand for a short time in a cylinder glass.

Table 17.

Measurements of Light in the Outer Broad (depth 9 m.) in 1940.

Date	Time	Weather conditions	k_s 1–4 m			k_s 4–8 m			Light at a depth of 4 m in percentages of light immediately below the surface			Light at a depth of 8 m in percentages of light immediately below the surface		
			blue	green	red	blue	green	red	blue	green	red	blue	green	red
24.6	13.50	Bright, calm	0.402	0.141	0.421	0.508	0.192	0.493	20.0	56.9	18.5	2.5	25.2	2.4
1.8	14.00	Bright, slight swell	0.711	—	0.700	0.599	0.373	0.592	5.8	22.5[1]	6.1	0.5	5.1	0.6
30.8	..	Slightly clouded slight swell . . .	0.634	0.312	0.620	—	0.266	0.619	7.9	28.6	8.3	0.6[1]	10.0	0.7
15.10	14.00	Dull, wind force 5, heavy sea	0.878	0.523	0.804	0.804	0.464	0.752	3.0	12.4	4.0	0.1	1.8	0.2

[1] Calculated on the assumption that the absorption coefficient was the same at all depths.

In Table 17 the measurements of light from the Outer Broad are listed, in Table 18 those from the entrance to the fjord. The material exclusively originates from the excursions through the fjord in 1940. On the excursions on August 1st and October 5th, 1940, the transparency for the volumes of water in the Outer Broad nearly corresponded to conditions on the same days in the Inner Broad. The weather was calm and the plankton was nearly identical in the two localities (see figs. 32—35). On August 30th, 1940, the transparency was appreciably greater in the Outer than in the Inner Broad. This was partly due to the fact that the plankton was richest in the Inner Broad, partly to the fact the rather unsettled weather conditions on that day had caused bottom material to be suspended over the very low depths in the Inner Broad, while this at any rate in a much lesser degree took place over the somewhat greater depths in the Outer Broad, where, moreover, the bottom is of a somewhat firmer nature. On June 24th, 1940, too, the transparency was somewhat greater in the Outer Broad than in the Inner Broad. On that day, which fell in quite a calm period, it was exclusively the amount of plankton which gave rise to the different transparencies.

At the entrance to the fjord the transparency was always considerably greater than in

Table 18.

Measurements of Light at the Entrance to the Isefjord (depth 7 m.) in 1940.

Date	Time	Weather conditions	k_s 1–4 m			k_s 4–6 m			Light at a depth of 4 m in percentages of light immediately below the surface			Light at a depth of 6 m in percentages of light immediately below the surface		
			blue	green	red	blue	green	red	blue	green	red	blue	green	red
24.6	12.30	Bright, calm	0.364	0.086	0.362	0.428	0.127	0.442	24.0	70.8	23.4	9.7	54.3	9.4
1.8	12.00	Bright, slight swell	0.415	0.152	0.439	0.414	0.228	0.534	19.0	54.5	17.3	8.4	33.3	5.8
15.10	11.30	Dull, nearly calm.	0.444	0.222	0.475	0.303	0.232	0 582	17.1	41.1	15.0	9.8	32.4	4.5

the fjord itself. This is due to the amounts of plankton always being much smaller there in connexion with the fact that the bottom consists of sand, which only under extremely unsettled weather conditions will be suspended in the water-masses.

Conditions of light in the water-masses at the entrance to the fjord presumably fairly correspond to conditions in the southeastern part of the Kattegat. Here I also on July 4th, 1942 (off the entrance to the Sound), found a submarine absorption coefficient, e. g. for the green rays, of 0.097 (0—17 m.) corresponding to the fact that the green light at a depth of 17 m. was 19 per cent. in proportion to the green light immediately below the surface.

Fig. 4 graphically shows the green light (percentage of green light immediately below the surface) at a depth of 4 m. at the three stations in the Isefjord area on the excursions in 1940. It is clearly seen how the transparency decreases towards the head of the fjord.

As will be discussed in more detail below, conditions of light in the Isefjord are so as to admit of plants living on the bottom everywhere, only apart from the deeper channels and holes. The fact that there is no benthos vegetation in the greater part of the Outer Broad and a considerable part of the Inner Broad is not due to conditions of light but to the nature of the bottom. On these areas, apparently empty of plants, there are, indeed, microscopical, autotrophic plants, e. g. diatoms and the blue-green alga *Oscillatoria*.

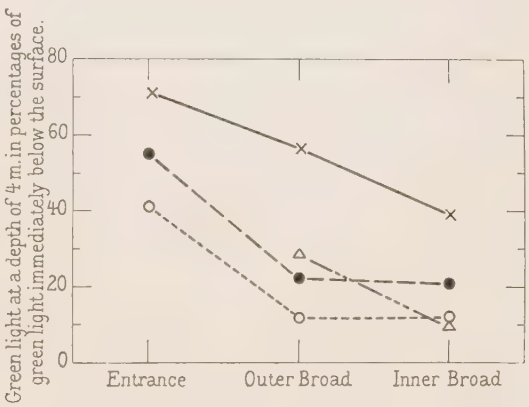


Fig. 4. Green light at a depth of 4 m. in percentage of green light at the surface of the Isefjord. 1940. × — × 24.6, o ——o 15.10, △—. . .△ 30.8, ●---● 1.8.

Chapter Two

PRODUCTION OF ORGANIC MATTER BY THE PHYTOPLANKTON IN THE ISEFJORD

A. Survey of the Investigations.

In a previous work (Steemann Nielsen, 1940) the production of phytoplankton in the Kattegat was discussed. It was shown that the two factors light and nutrient salts determine the size of the production. In the darkest months the light is the limiting factor for the production by the plankton algae, while the amount of nutrient salts determines the size of the production in the rest of the year. In the main the same factors determine the production of phytoplankton in the Isefjord. As regards the question how the supply of nutrient salts to the layers of water producing plankton takes place, the Isefjord, however, is essentially different from the Kattegat.

Water comparatively rich in nutrients is constantly carried into the Kattegat by the south-going under-current in the Danish waters. The average amount of phosphate-phosphorus in the water of the under-current is about 8 mg./m.^{3} and of assimilable nitrogen about 30 mg./m.^{3}. In the Kattegat a very considerable rise of deeper water takes place. According to Jensen 1940 this rise represents 2,300 cubic km. a year. In this way the surface layers producing plankton in the Kattegat are supplied with about 8 kg. phosphate-phosphorus and about 30 kg. assimilable nitrogen a year per ha. The rise of the water rich in nutrients does not, however, take place to the same degree over the whole area of the Kattegat. The waters along the coast of Jutland to a much higher degree than the waters near the coast of Sweden profit by the uprising water rich in nutrients. The plankton production is much greater in the western part of the Kattegat than in the eastern part. This is particularly evident in the months of summer (see further Steemann Nielsen, 1940).

The entrance to the Isefjord is in the eastern part of the Kattegat. The phytoplankton production immediately outside the Isefjord, therefore, is not of particularly great dimensions, particularly not in summer. The south-going under-current in the Danish waters, rich in nutrients, does not enter the Isefjord at all, particularly because the threshold in the entrance to the fjord is only 3 m. below the surface of the sea. The Isefjord therefore is not supplied with amounts of nutrient salts to any appreciable degree through the exchange of water with the Kattegat, which takes place in the form of surface water. The surface water in the Kattegat contains amounts of the nutrient salts only in the darkest months, as the plankton algae then, because of the poor conditions of light, cannot utilize the salts supplied. However, as the water-masses of the Isefjord during the winter contain much greater quantities of the nutrient salts, the exchange of water with the Kattegat actually effects a reduction of the amount of nutrient salts in the fjord.

As the area of precipitation of the Isefjord complex is situated in a eutrophic region which chiefly is arable land, the fjord is supplied with water from the land often rich in nutrients. The area of precipitation of the Isefjord itself, however, is small. Conditions are different as regards the Roskilde Fjord (see p. 13), for which reason we must here reckon with a considerable supply of nutrients through the freshwater supplied. No investigations of the plankton production have been made in the Roskilde Fjord. The investigations from the Inner Broad of the Isefjord, however, as will be discussed in detail below, show that the main source of

the nutrient salts is found in the fjord itself, as the nutrient salts are regenerated from organic substances by the action of bacteria, primarily at the bottom. As the action of bacteria is dependent on temperature, the regeneration of the nutrient salts increases with the temperature. The nitrogen and the phosphorus presumably mainly originate from the land, but the same quantities of nitrogen and phosphorus in this way again and again come to enter in the economy of the fjord. Only the quantities of these substances which every year for different causes are finally lost to the economy of the fjord need to be replaced. This replacement presumably mainly takes place by the supply of freshwater from the land. This is the case at any rate as far as the phosphorus is concerned.

It is the quantity of nutrient salts which throughout the year enters in the plant material that is primarily of interest. It is, however, impossible to determine this quantity directly in such an area as the Isefjord. Conditions are quite different in the Kattegat, where it is possible to determine the consumption of nutrient salts through the amounts of upwelling water added to the surface layer, at any rate in broad outline.

When the amount of the various nutrient salts in the water-masses of a marine area is determined through a year at definite intervals, it is only possible to see the surplus at each moment. In the surface layers in the Kattegat it is generally impossible in summer to show the presence of the nutrient salts even though it is possible in a different way to determine that the supply of these substances is considerable. The nutrient salts, however, apart from the darkest months, are used by the plankton algae as fast as they are supplied, so that there will be no surplus.

In the period of September 1941—September 1942 ammonia, nitrite, nitrate, and phosphate were determined once or twice a month, with the exception of January and February, at depths of 0 and 4 m. at the station in the Inner Broad off the naval station (depth 5 m.). Phosphate was, moreover, determined at this station from the beginning of March to September 1941. All these determinations are collected in Tables 12—13, p. 19—20. In the summer of 1940 phosphate was determined at the surface and immediately above the bottom (at Station II also at a depth of 4 m.) on four excursions through the Isefjord (Station I in the entrance, Station II in the middle of the Outer Broad, and Station III off the naval station in the Inner Broad; see the chart, fig. 1). These determinations are collected in Tables 12, 14, and 15.

After discussing the experimental investigations of the size of the plankton production we shall consider the amount of nutrient salts in the various seasons (see figs. 17—20).

In 1940 on the excursions mentioned above no investigations on the production of matter were made. Only water samples for the estimation of the quantity of plankton were taken. These were preserved by means of formaldehyde, 5 ml. 20 per cent. formaldehyde solution being added to 200 ccm. of water. Samples were taken partly from the surface, partly from a depth of about 1 m. above the bottom. Furthermore, a sample was taken from a depth of 4 m. at Station II in the middle of the Outer Broad.

In 1941 investigations of production on the basis of experiments on metabolism were started off the naval station in the Inner Broad. The Ministry for Naval Affairs had permitted us to use the station as our base and amongst other things placed a boat at our disposal. Mine Quartermaster N. I. Andersen assisted us in the work.

The winter of 1940—1941 was a typical ice winter like the preceding and following ones. On my first visit to the station on March 13th thick ice still covered the fjord. Plankton was collected and hydrographic measurements were made through a hole in the ice. At the end of the month the ice broke up, and when I visited the station again on March 27th—28th

the ice had disappeared completely. Besides the collecting of water samples and the preservation of these for the counting of phytoplankton I now made 24 hour experiments on the metabolism in surface water, which was distributed in small bottles at 15 ml. with glass stoppers and suspended at various depths (0.3, 1, 2, and 4 m.), two bottles at each depth. In a few series of experiments bottles were also placed at a depth of 5 m. Two bottles wrapped in black material were furthermore suspended at a depth of 4 m. The metabolism was determined by means of determinations of oxygen according to a modified Winkler method (see KROGH and LANGE 1932). Determination of oxygen in the water was also made at the start of the experiment. Photosynthesis and respiration were calculated as glucose per litre of water. Furthermore it was calculated on the basis of the whole series how much glucose per square m. of surface was produced (gross production) and decomposed by respiration per 24 hours in the locality in question, which may be considered typical of the whole Inner Broad.

Similar experiments with metabolism were made twice a month during the rest of 1941 (in November and December, however, only once).

About Christmas the ice again became permanent, to disappear only in April 1942. In March of this year collection of plankton was made through a hole in the ice. The experiments

Table 19.

Experiments with Metabolism in Surface Water in the Inner Broad 1941—1942.

Experiment started	Weather conditions	Percentage of green light at a depth of 4 m in relation to the surface	mg glucose formed by photosynthesis per litre and 24 hours (gross production = rea photosynthesis)					mg glucose decomposed by respiration per litre and 24 hours
			0.3 m	1 m	2 m	4 m	5 m	
27. 3.1941—14.30..	Slight-dense cloud, strong wind and heavy sea	..	0.69	—	0.19	0.05	0.015	0.21
8. 4.1941—13.45..	Very bright, off-shore wind....	..	0.24	0.32	0.32	0.25	0.15	0.08
24. 4.1941—13.40..	Bright, light on-shore wind ...	..	0.17	0.23	0.22	0.18	0.13	0.05
7. 5.1941—13.50..	Bright-slight cloud, wind from the north.....	..	0.26	0.36	0.30	0.18	0.13	0.08
28. 5.1941—19.55..	Bright, on-shore wind	15	—	1.71	1.53	0.85	0.56	0.49
11. 6.1941—19.05..	Slight cloud, off-shore wind ...	16	—	0.36	0.36	0.32	..	0.24
24. 6.1941—20.15..	Bright, calm.....	51	—	0.65	0.65	0.62	..	0.42
15. 7.1941—19.05..	Bright-cloud, calm.....	25	0.71	0.74	0.76	0.52	..	0.47
29. 7.1941—19.15..	Cloud, slight rain, nearly calm	20	1.22	0.92	0.82	0.53	..	0.44
13. 8.1941—19.05..	Rain, off-shore wind.....	5	2.16	1.15	0.70	0.20	..	0.71
26. 8.1941—19.05..	Slight cloud, off-shore wind ...	9	0.93	0.91	0.79	0.41	..	0.27
10. 9.1941—19.00..	Showery, slight cloud.....	12	1.28	1.14	1.07	0.55	..	0.29
29. 9.1941—13.15..	Bright, on-shore wind, heavy sea	8	0.63	0.89	0.71	0.24	..	0.14
13.10.1941—13.30..	Bright-slight rain, off-shore wind	27	0.41	0.31	0.23	0.13	..	0.09
27.10.1941—14.00..	Slight cloud, calm after gale...	26	0.21	0.20	0.13	0.11	..	0.11
18.11.1941—14.00..	Foggy, calm	32	0.15	0.12	0.05	0.01	..	0.04
27. 4.1942—14.00..	Bright, slight cloud, on-shore wind, heavy sea.....	..	0.07	0.12	..	0.06	..	—
18. 5.1942—19.10..	Bright-cloud, off-shore wind ...	..	0.29	0.37	0.22	0.11	..	—
15. 6.1942—19.30..	Rain, nearly calm.....	..	0.36	0.23	0.11	0.04	..	0.11
20. 7.1942—19.00..	Dull-rain, off-shore wind	..	1.05	1.21	0.79	0.68	..	0.46
24. 8.1942—13.30..	Bright, calm.....	..	1.13	1.24	0.93	0.60	..	0.38

with metabolism then were continued in April and the following months till the end of the summer, although only once a month. The results of all the series of experiments are given in Table 19. Every value stated is the average of two parallel experiments. The results of a number of selected series of experiments are graphically represented in figs. 5—11.

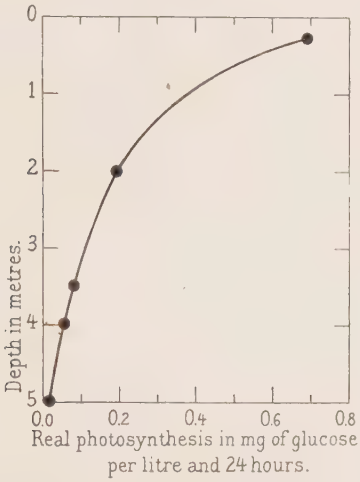


Fig. 5. Photosynthesis on March 27th—28th, 1941.

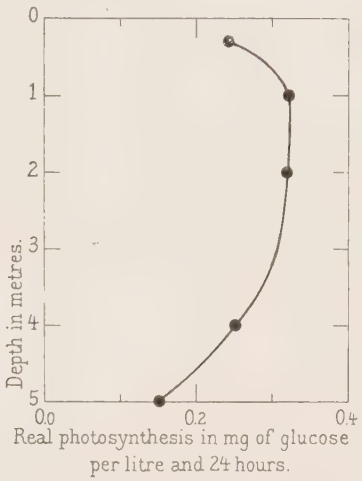


Fig. 6. Photosynthesis on April 4th—5th, 1941.

The investigations then were continued exclusively with the collection of plankton. In the winter of 1942—43 the Isefjord was not frozen over. In 1943 plankton (preserved water samples) was collected about every fortnight until the end of August when the investigations had to be concluded as the Danish military and naval forces were interned and the Germans took over the naval station.

To illustrate the phytoplankton production in the Inner Broad we have thus both experiments on metabolism (two years) and quantitative determinations of plankton (four years).

B. Theoretical Discussion of the Experimental Methodics.

The determination of photosynthesis and respiration per surface unit for the various 24 hours must be considered as certain (see Steemann Nielsen, 1932). Matters are different when on the basis of e. g. experiments made twice a month we are to determine the production of the whole month. In the first place the amount of plankton often changes very considerably within a fortnightly period, so that the production of matter varies for this reason. The investigations in the Sound 1932—1933 therefore were made once a week (Steemann Nielsen, 1937). For practical reasons this was not possible in the case of the investigations in the Isefjord.

Weather conditions in the period of 24 hours in which the experiment is made is, moreover, of very great importance for the size of the production of matter. First and foremost conditions of light play a role. The light varies greatly from day to day. In 1939 438,000 lux/hours were measured in Copenhagen on the lightest day in July, while on the darkest day in the same month 52,200 lux/hours were measured (according to Romose, 1940). On January 24th, 1938, 3,400 lux/hours were measured, while two days before 38,700 lux/hours were measured. The cloud ceiling thus both in summer and winter can cause an average reduction of the light-

intensity to about $^1/_{10}$. The optimum photosynthesis of the plankton algae is reached about 7,000 lux (Steemann Nielsen, 1937), half of optimum assimilation at about 2,000 lux. In July the average light-intensity at noon in Denmark is 45,000 lux (according to Boysen Jensen, 1943). In January the average light-intensity at noon is 6,000 lux. Already at the surface a

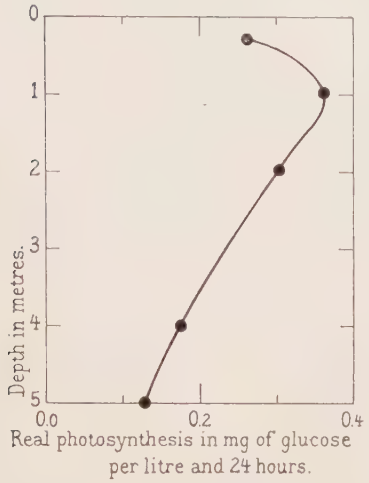


Fig. 7. Photosynthesis on May 7th—8th, 1941.

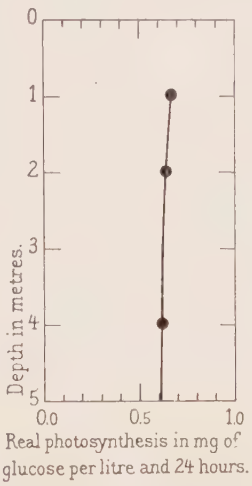


Fig. 8. Photosynthesis on June 24th—25th, 1941.

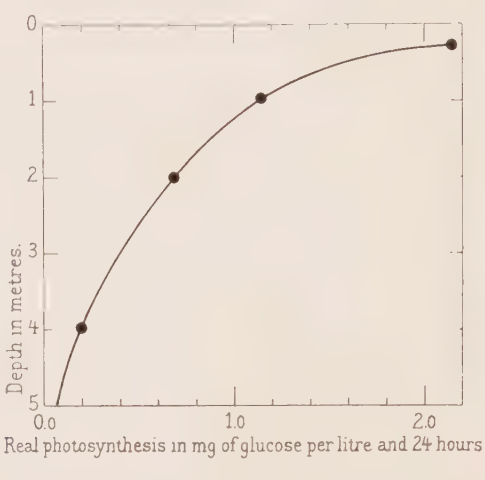


Fig. 9. Photosynthesis on August 13th—14th, 1941.

considerable cloud ceiling is in winter of absolutely decisive importance for the production of matter. In summer the cloud ceiling is not of so decisive importance for the production of matter immediately at the surface. The production of matter is appreciable reduced for that cause only on extremely dark days.

One fact is of importance in this connexion. At more than 20,000 lux the light is too strong for the plankton algae; see e. g. fig. 12, Steemann Nielsen, 1944. In sunshine in summer the photosynthesis therefore is somewhat greater a little distance down in the water than immediately below the surface (see figs. 6, 7, and 10). A minor cloud ceiling therefore by no means has a reducing effect on the production of matter by the plankton immediately at the surface, but a promoting effect.

In the case of the slightly deeper layers conditions are different. Here the transparency of the water also plays a decisive part. Especially in such a water as the Inner Broad, where the transparency of the water-masses varies extraordinarily, this fact must be highly taken into consideration. If we compare e. g. the submarine conditions of light on June 25th, 1941, with conditions on August 14th, 1941 (see Table 16, p. 24), we find in the former case at a depth of 4 m. 51 per cent. of the green light at the surface, whereas in the latter case we find 5 per cent. only. The green light has been used in this example as the rays of this colour in such an area as the Isefjord penetrate farthest down and therefore in the somewhat deeper layers become of absolutely decisive importance for the photosynthesis of the plankton algae. Furthermore a curve for the distribution of energy in sunlight shows a maximum for green light (see Steemann Nielsen, 1944, fig. 4).

If we start from the average intensities of light in June and August at various times of the day (Boysen Jensen, 1943, fig. 78), and put the actual optimum photosynthesis per hour at a, and use the curve showing the dependence of photosynthesis on light (Steemann

Nielsen, 1937, fig. 6), the actual photosynthesis on June 25th, 1941, at a depth of 4 m. becomes about 15 a. For August 14th, 1941, the corresponding value at a depth of 4 m. becomes about 5 a. If we put the quotient of optimum actual photosynthesis : respiration for 24 hours at 8, the respiration for 24 hours in both cases becomes 3 a. Thus, at a depth of 4 m., there would not on August 14th, 1941, appear any appreciable surplus of organic matter during the metabolism of the plankton algae (the compensation point being at a depth of about 5 m.), whereas on June 25th we should at a depth of 4 m. have a considerable surplus, which would be no greater in any layer of water higher up. Near the surface we should even expect a somewhat smaller surplus, as the too bright light will here cause a reduction of the intensity of photosynthesis, as stated above. It is obvious that the production of matter by the plankton algae per surface unit becomes considerably greater on June 25th than on August 14th, even if we reckon with the same amount of plankton and with standard illumination in the surface in both cases.

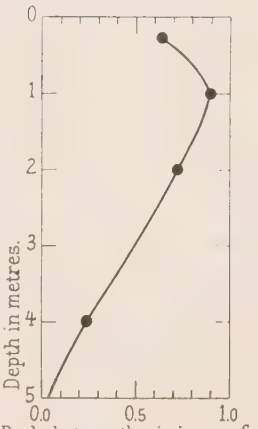


Fig. 10. Photosynthesis on September 29th—30th, 1941.

How do these theoretical calculations of the relative production of matter on the two days agree with the experimental measurements of the production made on the two days?

Fig. 8 shows the real photosynthesis at the various depths per 24 hours after the experiment of June 24th—25th, 1941. The sun was shining on both days. The light-intensity at the surface thus was somewhat greater than in the average for June. In accordance with this and with the above theoretical calculations we therefore find that the intensity of photosynthesis at a depth of 4 m. is the same as at a depth of 1 and 2 m.

Fig. 9 shows the real assimilation at the various depths in the 24-hour experiment on August 13th—14th, 1941. Both days were rainy; so the light-intensity at the surface was low. In accordance with this and the poor transparency of the water there is an increasing fall in the intensity of assimilation from the surface down. Already at a depth of about 1 m. the assimilation intensity had dropped to half, at a depth of 4 m. it had dropped to $^1/_{10}$. When the transparency of the water-masses is poor, the variation in the amount of light striking the surface, gets a particularly great influence on the production of matter per surface area in the Isefjord. As of course it is impossible always to make the experiments on days with a standard illumination, a single determination of the production of matter made on an extremely dark day of a period may very well deviate considerably from the average production of matter in this period. The determination of metabolism on August 13th—14th thus gives too low a value for the production of matter in the middle of August 1941. This is not, however, of any appreciable importance for a calculation of the production of matter during the whole summer period, since, as appears from fig. 13, the summer maximum for the production of matter in the Inner Broad has a duration of about 4 months. Matters are different in the case of a maximum of a very short duration, such as the spring maximum of 1941. Only a single series of experiments was made at the peak of this maximum (the experiment on March 27th—28th, 1941). During this series the weather was very cloudy

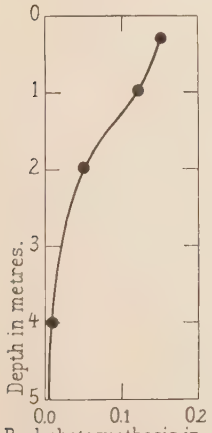


Fig. 11. Photosynthesis on November 18th—19th, 1941.

and, what was still more significant, the water was very turbid, as the bottom material because of an on-shore gale had been raised. The curve in fig. 5 shows that the intensity of photosynthesis decreased very much from the surface down.

During the days immediately before this series of experiments was made, the weather was brighter and no on-shore gale had made the water-masses particularly turbid. During those days the production of matter must have been much greater than on March 27th—28th. Fig. 12 shows the production of matter in 1941 per 24 hours and litre of water at the best depth (i. e. a depth of 0.3 m. or, if the effect of too bright light asserted itself, at a depth of 1 m.). In this curve the spring maximum stands out clearly. The curve in fig. 18 in Steemann Nielsen 1944 is a combination of this curve and the proper curve of production of matter (fig. 13). In this way the characteristic spring maximum was not concealed.

C. Size of the Production of Matter.

Fig. 12 shows the production of matter per square m., calculated from the experiments, for 1941 (fully drawn line). It is seen that there were three maxima. First the spring maximum proper in March, which, as already mentioned, was actually greater than appears from the

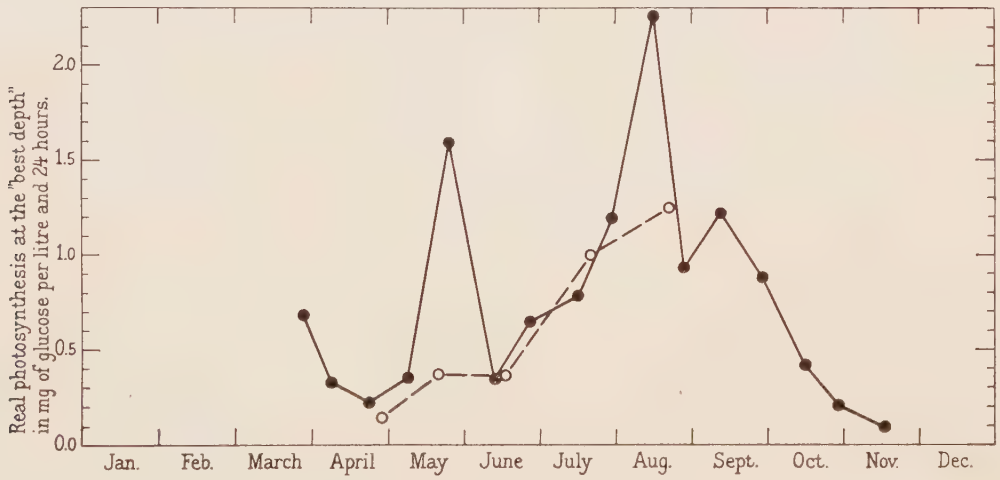


Fig. 12. Photosynthesis at the best depth in 1941 and 1942.

figure. Then follows a minimum in April to the beginning of May, after which a considerable maximum sets in at the end of the month. This maximum, which is of short duration, is followed by another minimum. The summer maximum proper, which continues till the end of September, does not set in until the end of June. In the course of the autumnal months the production decreases greatly.

Fig. 13 besides the curve for the production of matter per square m. of surface in 1941 also shows the curve drawn on the basis of the experiments in 1942 (the broken line). It is seen that in 1942 there was a summer maximum of a similarly long duration as in 1941. At the investigations on September 29th, 1942, it was not possible to suspend the bottles for the investigations of the production of matter because of a gale from the southeast. However, from the considerable quantities of plankton present on that day—see e. g. fig. 25—it appears that the summer maximum was in full swing as at the same time in the previous year.

Fig. 13 shows a very high maximum of short duration for the production of matter at the end of May 1941. A similar, though insignificant maximum was ascertained in 1942. As determinations of production were made only once a month during that year, there is, of course, a possibility that this maximum was actually of a very different order of magnitude.

A calculation of the real photosynthesis of the plankton algae (apparent photosynthesis + respiration, — the respiration of bacteria and small zooplanktonts enter in the calculation) during the whole of 1941 per square m. of surface at the station (at a depth of 5 m.) in the Inner Broad gives 584 g. glucose. As the depth outside the shoals is generally 7 m. in the Inner Broad, but on the shoals generally considerably less than 5 m., a photosynthesis (gross

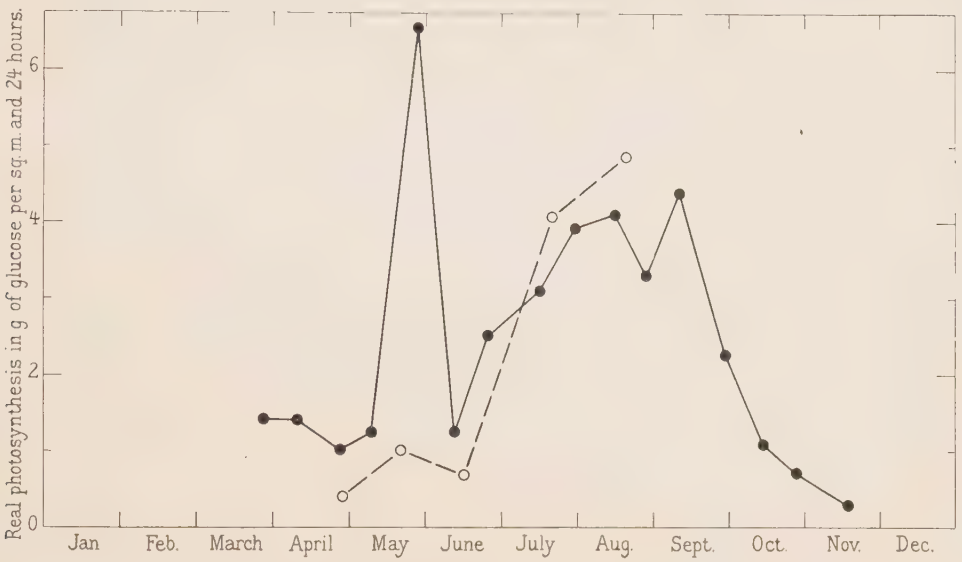


Fig. 13. Production per square metre of surface in 1941 and 1942.

production) of 600 g. glucose per square m. and year for the whole Inner Broad is at any rate of the correct order of magnitude.

The plankton algae respirates like all other plants. At the same time as they build up organic matter, they also decompose organic matter. In order to determine the surplus of organic matter (as expressed in glucose) in the metabolism of the plankton algae it is absolutely necessary to know the total respiration in the water. This value, however, besides the respiration of the plankton algae, as mentioned above, also comprises the respiration of bacteria and zooplankton. Therefore it is not possible to use the values of respiration found as representatives of the respiration of the plankton algae.

The ratio between the real photosynthesis and the respiration per square m. of surface is plotted along the ordinate in fig. 14. The ratio between the real assimilation at the best depth (0.3 or 1 m.) and the respiration is plotted along the ordinate in fig. 15. In both cases the months (1941) are plotted along the abscissa.

It is seen in fig. 14 that in the whole period in 1941 in which experiments were made there was a surplus in the metabolism of the water-masses. It should, however, be noted that larger animals—fish and bigger zooplankton organisms -are not included in the investigations. In June, July, and the beginning of August the surplus of production of organic matter in

relation to the decomposition is not particularly great (20—80 per cent. surplus). This is at any rate to a very high degree due to the zooplankton. In the beginning of June 1941 a great many larvae of mussels were hatched. According to Dr. THORSON's countings (see 42)

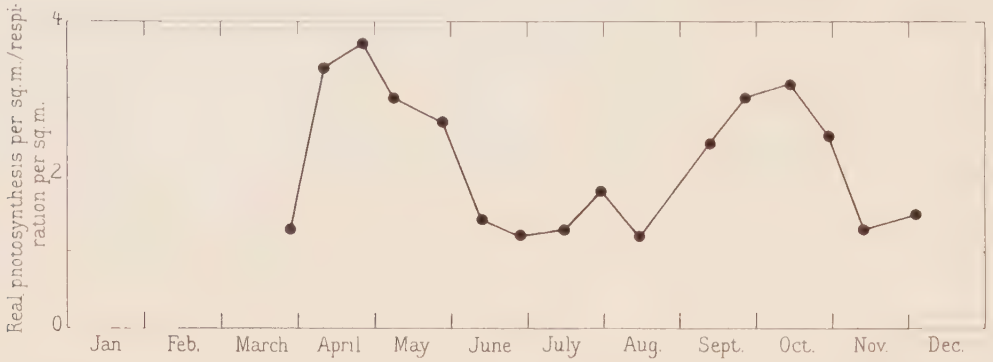


Fig. 14. Relation between real photosynthesis per square metre and respiration per square metre (24 hours).

3,000 such larvae per litre were present in the middle of June, an overwhelming number. In the course of July—August these larvae settled or perished.

In April—May and in September—October about three times as much organic matter was produced per surface unit as was decomposed there at the same time. The main part of the decomposition of matter must now be due to the respiration of the phytoplankton itself. The quotient

Fig. 15. Relation between real photosynthesis at the best depth and respiration (24 hours).

optimum real photosynthesis : respiration (in the plankton algae) may be put at 10—20, which, to judge from all investigations, is at any rate of the correct order of magnitude. In 24-hour experiments, in which, in the first place, the night also enters and in which there is no optimum photosynthesis in the somewhat deeper layers even by day, we must then reckon with a considerably smaller quotient than 10 for the ratio of the real assimilation of the plankton algae to their respiration per surface unit and per 24 hours. If we put this quotient at 5, it is un-

doubtedly not too high, at any rate not for April and September, when the night is comparatively long. The main part of the respiration of the water must therefore at these times be supposed to be due to the plankton algae, as the quotient, as stated above, is 3—4 for April, May, and September, October. If we as average for the whole year put the quotient for the autotrophic plankton algae at 4 (in my 1937 paper it was put at 6), the net production is 75 per cent. of the gross production, i. e. 450 g. glucose per square m. and year.

D. Factors Determining the Production of Matter.

A comparison between the curve of production of matter for 1941 with the curve of temperature for the surface water in the Inner Broad in 1941 (see fig. 16) shows that the two curves on the whole are parallel. It is quite improbable that it should be the temperature which

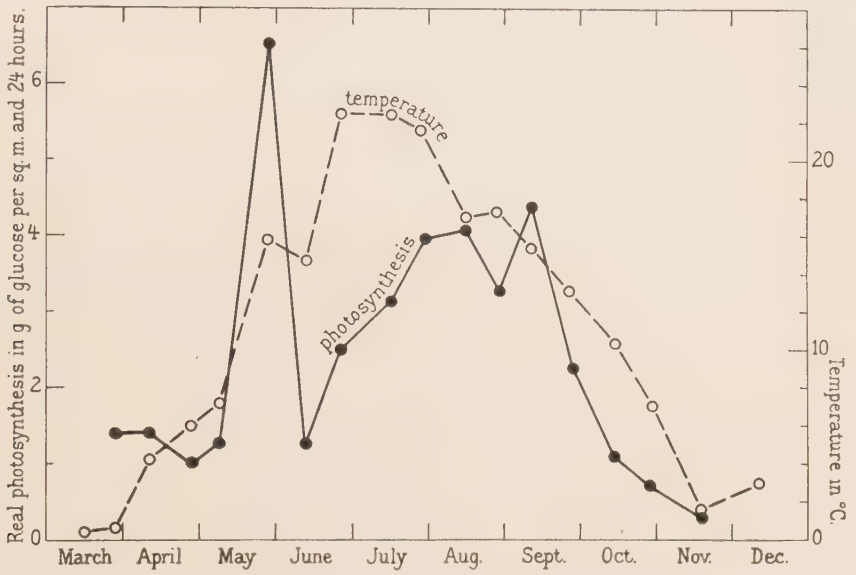


Fig. 16. Production of matter and temperature 1941.

is the factor directly determining the production of phytoplankton. It is true that the photosynthesis at higher light-intensities is dependent on temperature (see e. g. Steemann Nielsen, 1942, p. 87). Experiences from the investigations of the metabolic production of the phytoplankton in the Scandinavian waters, however, decidedly do not seem to indicate such a direct dependence on the temperature (see e. g. Steemann Nielsen, 1940).

The curve of illumination is to a certain degree parallel to the curve of the temperature in the water, but in fact to a certain degree only. Conditions of light about the vernal and the autumnal equinox thus are in agreement, whereas the temperature in the water at the autumnal equinox is generally about 10°C. higher than the temperature at the vernal equinox. The low values for the production of matter in April and the beginning of May thus are inexplicable if the light should be the decisive factor for the size of the production of matter in that season.

On the other hand a comparison between the curve of production by the plankton for 1941 with the curve for the amount of phosphate in the water in 1941 (fig. 17) shows that in

April of that year it was not possible at all to show the presence of free phosphate in the water. It is not possible to show the presence of this substance till May; in June—August there are relatively great quantities in the water. In principle the same appears from the curve for 1942, and the determinations from 1940, too, show the presence of comparatively great amounts of phosphate in the height of summer. In the spring of this year no determinations were made. The curve with the monthly means for the years 1940—1942 (fig. 18) shows conditions particularly clearly. As already pointed out on p. 21 the amount of free phosphate does not tell

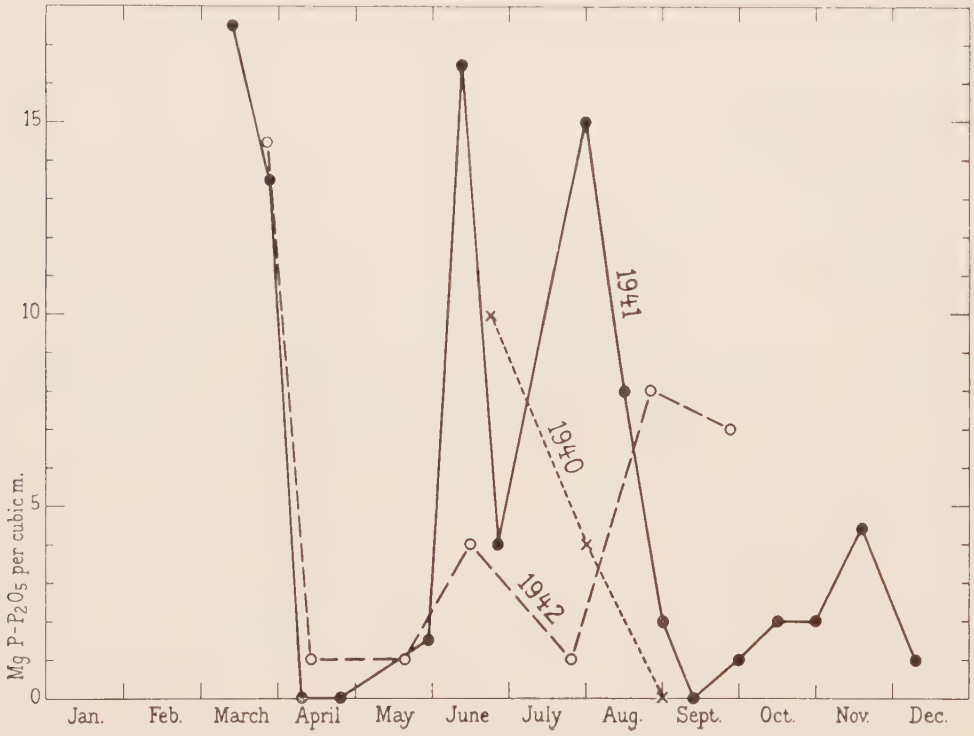


Fig. 17. Phosphate in 1940, 1941, and 1942 in the Inner Broad. Average of the determinations at the surface and at 5 metres.

anything direct about the supply of phosphate, but a combination of the curve of production of matter with the curve of phosphate will show the principal lines for the supply of phosphate. When in April the production of matter is low, the consumption of phosphate thus being relatively low, and when at the same time there are no quantities of phosphate in the water, the supply of phosphate to the water must be low. On the other hand, when in the height of summer, simultaneously with a great production of matter, which consumes relatively great amounts of phosphate, there are also comparatively great quantities of phosphate in the water, the supply of phosphate to the water must be comparatively great.

The cause of the greater supply of phosphate to the water-masses in the height of summer is that free phosphate is regenerated at the bottom of the sea by the decomposition by bacteria of organic substances containing phosphorus. This phosphate is carried into all water-masses by the vertical current, which because of the low depths in the Isefjord is generally of a very

considerable extent. Apart from periods of very calm weather conditions, the water-masses from bottom to surface are mixed nearly evenly. The water-masses are stabilized only in very calm periods. But then we just in the deeper layers find much greater quantities of phosphate than in the surface layers. It is typical of such conditions that on the excursion on June 24th, 1940, we found 15 mg. phosphate-phosphorus per cubic m. near the bottom and 3 mg. per cubic m. at the surface in the Outer Broad. In the Inner Broad the corresponding figures were 15 and 5 mg. (see Tables 12 and 15). The cause of the great regeneration of phos-

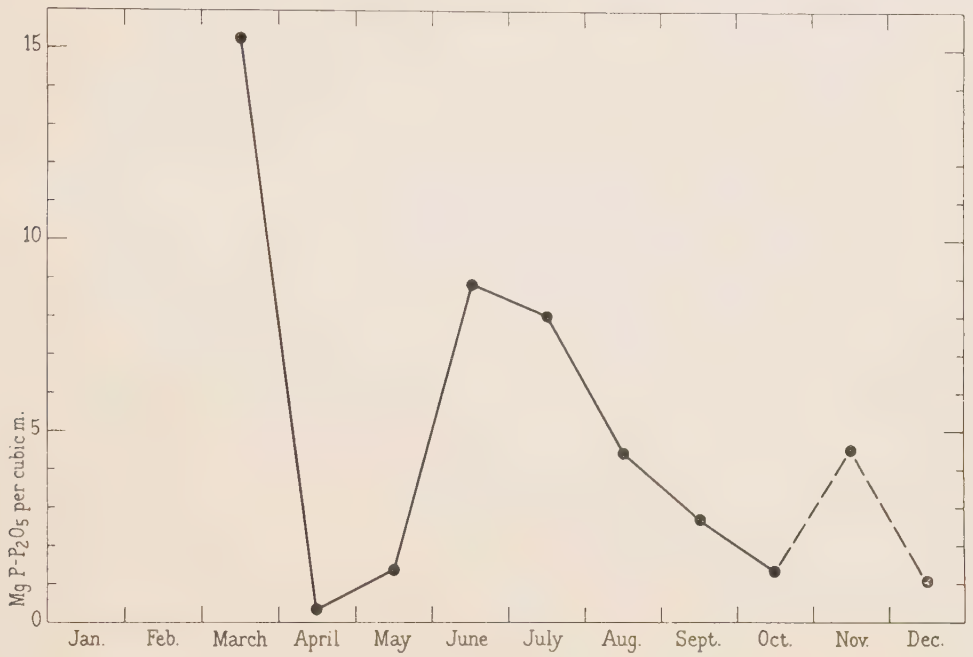


Fig. 18. Monthly means of phosphate in the Inner Broad.

phate at the bottom in the height of summer is the high temperature, the action of bacteria being highly dependent on temperature. As the production of matter in summer is primarily regulated by the amount of nutrient salts (nitrates, phosphates), the curves for temperature and production of matter in the Isefjord run parallel. No doubt a redevelopment of phosphate takes place by bacterial decomposition of organic substances containing phosphorus which are dissolved in the water-masses. However, from conditions in the periods of stagnation, when the main quantity of phosphate is found in the layers near the bottom it must be assumed that the redevelopment of phosphate in the bottom itself is the chief cause of the production of phosphate in the Isefjord.

Generally the curves for assimilable N (nitrate, nitrite, ammonia) and phosphate-phosphorus in the sea run fairly parallel. Generally there are about 9 times as much N as P (Wattenberg, 1938). When phosphorus is at a minimum, nitrogen is also generally at a minimum. This was, however, by no means the case in the Inner Broad of the Isefjord. In April 1940, when phosphate was at a minimum (about 1 mg. phosphate-phosphorus per cubic m.) 240 mg. nitrate-nitrogen, 175 mg. ammonia-nitrogen, and 8 mg. nitrite-nitrogen per cubic m. were found simultaneously (see figs. 19 and 20). Even though the requirements of the plants for nitro-

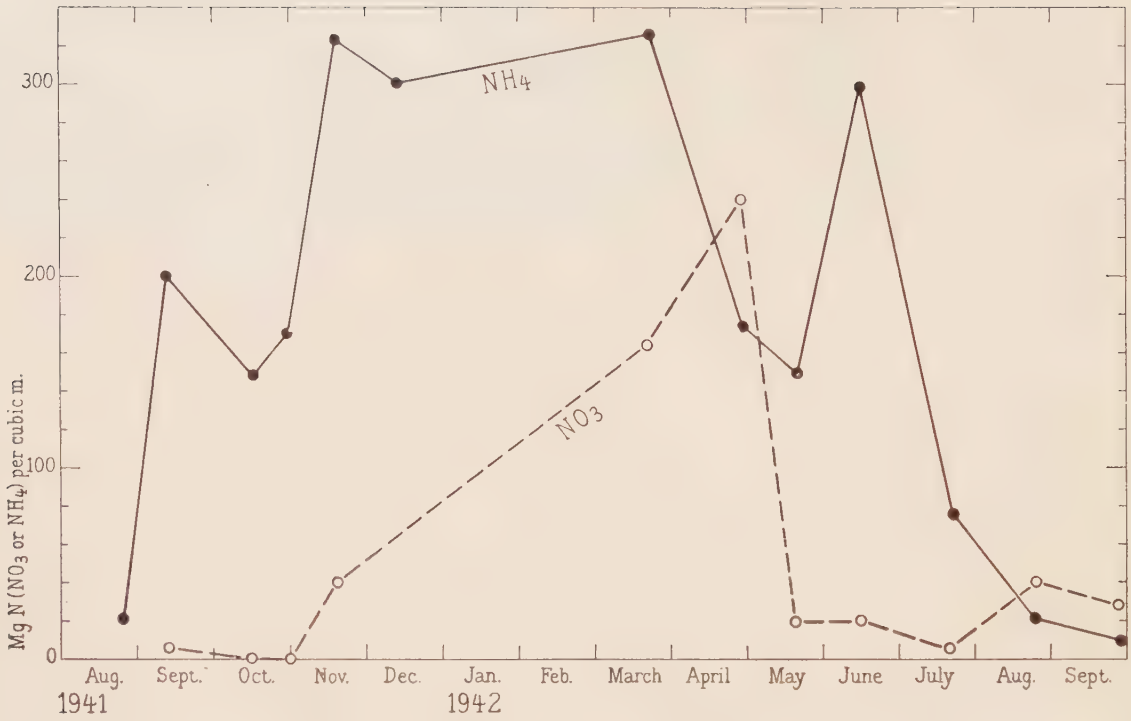


Fig. 19. Nitrate and ammonia 1941—1942 in the Inner Broad. Average of the determinations at the surface and at 5 metres.

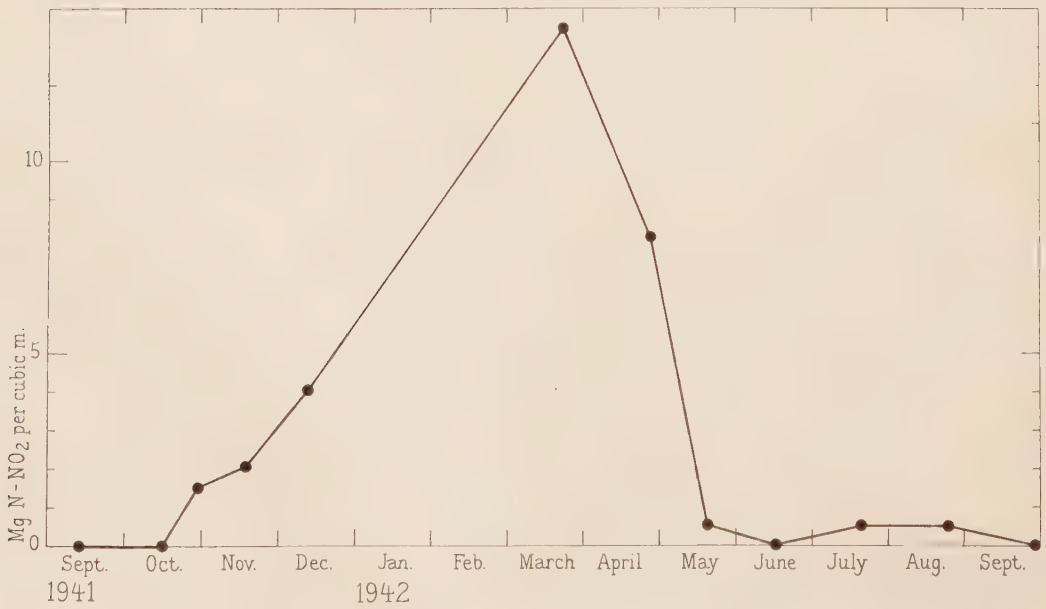


Fig. 20. Nitrite 1941—1942 in the Inner Broad. Average of the determinations at the surface and at 5 metres.

gen are about 9 times as great as those for phosphorus (Wattenberg, 1938), the figures show that the nitrogen is not at a minimum at all. So great quantities of assimilable nitrogen generally are not found in surface layers in the sea, not even in very eutrophic areas.

The lowest amount of assimilable nitrogen was measured in September 1942 (about 35 mg N/m³), the highest amount in March 1942 (well over 500 mg. N/m.³, as the average for surface and a depth of 5 m., 325 mg. of which as ammonia, 165 mg as nitrate, and 14 mg. as nitrite per cubic m.).

Nitrite was only found in the period of November—April. Its maximum was in March (14 mg. N/m.³). In proportion to the amounts of ammonia and nitrate the small amounts of nitrite are of no biological importance. Indeed, nitrite only constitutes an intermediate stage in the transformation of ammonia into nitrate.

The amounts of assimilable N compounds in the Inner Broad of the Isefjord are very great as compared with normal conditions in the sea, the oceans as well as the coastal waters. In the surface layers of the Kattegat there are but insignificant quantities of nitrate-nitrogen, and even in the deepest layers of water the presence of more than 100 mg./m.³ has never been shown (Steemann Nielsen, 1940). In the surface of the Atlantic between Iceland and the Faroes about 100 mg. N_{NO3} per cubic m. is found immediately before the start of the spring maximum of the plankton. Ammonia was not determined in the Kattegat at the investigations mentioned above; but in the Kiel Bay off the Kieler Förde Wattenberg and Meyer in 1936 at investigations throughout the year found a maximum of well over 20 mg. ammonia-nitrogen per cubic m. both at the surface and near the bottom. In the open ocean the amount of ammonia is of completely subordinate importance.

The Inner Broad seems to have points of similarity to the brackish areas near Rügen (primarily Grosser Jasmunder Bodden) as regards nitrogen. It is true that ammonia was not determined at the investigations made there (Gessner, 1937). But nitrate was found in winter in amounts up to 100 mg. N/m.³. The determinations were made in an ice-free winter when phytoplankton was present in great quantities throughout the season. Therefore it is probable that at the end of winters in which phytoplankton was at a minimum because of ice covered with snow (lack of light) there are considerably greater quantities of nitrate than detected in the winter of 1932—1933 in this area.

At the end of August 1941 when the investigations of the content of ammonia in the Inner Broad of the Isefjord were started, an average (the surface and a depth of 4 m.) of 20 mg. N_{NH4} per cubic m. was found. But as early as the middle of September the amount of ammonia had increased to 200 mg./m.³. Great amounts of ammonia were present in the autumn of 1941 —from November even more than 300 mg. N/m.³. 325 mg. ammonia-nitrogen per cubic m. were measured at the end of March 1942 when the ice was still covering the fjord. In the course of April—May the amounts of ammonia dropped to about half. In June there was a rise to about 300 mg. N/m.³, but in the summer this amount dropped greatly. By the end of September the amount of ammonia had dropped to about 10 mg. N/m.³. The curve of ammonia (fig. 19) thus shows a minimum proper only in late summer.

Nitrate (fig. 19) in September and October was found in very small amounts; in November it had increased to 40 mg. N/m.³. 165 mg. nitrate-nitrogen per cubic m. were found under the ice at the end of March 1942. When the ice disappeared at the beginning of April and the spring maximum of phytoplankton began to assert itself, the amount of nitrate still increased (at the end of April 240 mg. N_{NO3} per cubic m.). Then it dropped fast. In the summer months there were generally about 20 mg. nitrate-nitrogen per cubic m. (5—40 mg.).

The nitrate develops by oxidation of ammonia through nitrite. In the period from the end of March to the end of April (the period of the spring maximum of phytoplankton) the amount of ammonia was reduced by 150 mg. N/m.^{3}. Simultaneously the amount of nitrate increased by 75 mg. N/m.^{3}. The phytoplankton thus in this period used 75 mg. N/m.^{3} besides the amounts of assimilable nitrogen which during this period had redeveloped from organic nitrogen compounds, first of all originating from the sea floor. Nitrogen during this period, however, was not at all present as a minimum factor. The fact that the production of matter by the phytoplankton was low by the end of April was due to the phosphate, which had now got at a minimum. Nitrogen cannot at all be considered a minimum factor at any time during the period of September 1941 to September 1942. As shown above, this role falls to the phosphate. This is most obvious in the period immediately after the spring maximum of the phytoplankton.

For about three months thick ice covered the Isefjord in each of the winters of 1940—1941 and 1941—1942. During the greater part of the winter the ice, moreover, was covered with snow. Light penetrates such a layer of snow to a very slight degree, only. There were extremely bad conditions of light to the phytoplankton. During the latter part of the ice period of each year the layer of snow on the ice, however, melted by the action of the sun. Though the melted snow froze again, the possibility of the light to penetrate to the water-masses below the ice was increased many times. It actually proved at the investigations of the plankton under the ice at the middle of March 1941 and at the end of March 1942 that a quantitatively significant phytoplankton crop had already developed (see figs. 21 and 25); but it is unimaginable that any phytoplankton of importance should have developed in January and February of these years. Therefore, even though only small amounts of nutrient salts regenerate at that time because of the low temperatures, the amounts still increase to a considerable degree. From December 1941 to the end of March 1942 the average amount of phosphate rose from 1 to 15 mg. P per cubic m., and the total amount of nitrate-, nitrite-, and ammonia-nitrogen rose from 360 to 500 mg/m.^{3}.

The amounts of nutrient salts accumulated provoke an intense growth of phytoplankton as soon as conditions of light improve, i. e. when the ice becomes transparent or—still better—disappears completely. The amount of phosphate, which was not particularly large, however, will soon be consumed and the spring maximum of the phytoplankton will be of short duration. Then the production of plankton depends on the amounts of phosphate regenerated by bacteria. As the temperature is still low little phosphate is found. The production of phytoplankton, therefore, is only low. Only when the temperature in the water-masses increases, the action of the bacteria regenerating phosphate thus being increased, the production of phytoplankton and thus the production of matter increases again.

At the end of May 1941 the temperature of the water in the Inner Broad had risen to about 15°C. The production of matter by the phytoplankton simultaneously had reached a very great height. Then a considerable fall in the production of matter followed in the first half of June although the contents of both phosphate and ammonia had increased (see figs. 17 and 19). In the course of June—July the production of matter again reached high values. The minimum at the beginning of June was presumably first of all due to the appearance of the zooplankton. Whereas the amount of this was very small as late as the end of May, great amounts were present from the beginning of June. Particularly larvae of mussels were very numerous then. As mentioned above, about 3,000 per litre were found according to Dr. Thorson's countings. These larvae live on phytoplankton of the nannotype and must make a great inroad on

the vegetation of plankton algae. The larger diatoms are not eaten by the mussel larvae. As we shall see, the amount of diatoms had also dropped considerably at the beginning of June. This cannot, of course, be attributed to the mussel larvae. It is not easy to tell how this problem is to be explained.

The disappearance of the diatoms is possibly due to the silicate, which during a violent production of diatoms is consumed completely. (The problem of silicium will be discussed in detail on p. 46).

In mild winters when the Isefjord does not freeze over, the "spring maximum" of the phytoplankton may appear at a much earlier time than in winters with an ice-cover of long duration. This was the case in the mild winter of 1942—1943. No experiments for the purpose of investigating the production of matter were made, but the development of the phytoplankton was observed by means of quantitative countings. Fig. 29 shows that there was a very distinct maximum for diatoms in the first half of February. As early as the beginning of March the "spring maximum" was over. At this time the amounts of phosphate accumulated during the darkest time were presumably consumed, so that the production of plankton was exclusively based upon the amounts of phosphate which constantly regenerated. As the temperature was still low, this regeneration was slight. It only increased during May when the heating of the water-masses set in. Then the amount of plankton increased, as seen in fig. 29.

The production of phytoplankton may set in at a very early date in such a shallow water as the Isefjord. In the Kattegat, where the greater depths are compensated by the strongly stabilized water-masses, the production of plankton may start at a similarly early date (see Steemann Nielsen 1940). In our latitudes the quantities of light striking the surface of the sea are considerable as early as the end of January in periods with little cloud.

In the week of January 26th to February 1st, 1938, the daily average quantity of light in Copenhagen was 45,000 lux/hours according to Romose 1940 Table 23 b. The length of the day at that time is about 8 hours. On a bright day at the end of January a light-intensity of more than 7,000 lux in 5 hours of the day was measured. An optimum intensity of photo-synthesis is reached by the plankton algae at about 7,000 lux.

The results of the investigations of the factors determining the production of phytoplankton in the Isefjord may be summarized as follows. Light is the regulating factor only in the darkest period of the year, in November—January (or in ice winters until the ice cover of the fjord has disappeared). Outside this period the supply of phosphate determines the size of the production of matter. As the regeneration of phosphate depends on temperature, the size of the production of matter thus depends on temperature. A minor "spring maximum" of the production of matter is due to the accumulation of some phosphate during the period when the plankton algae because of the insufficiency of the quantity of light cannot manage to consume all the phosphate regenerated (although small amounts because of the low temperature). In the early summer zooplankton, primarily larvae of mussels, greedily consumes the plankton algae, a fact which has an inhibiting influence on the size of the production of matter by the phytoplankton.

A factor which is very important to the photosynthesis of the plankton, viz. the content in the water of assimilable C, i. e. CO_2 and HCO_3-ions, has not been considered at all in the preceding sections. Presumably most of the marine plankton algae, like the freshwater species *Scenedesmus quadricauda*, can assimilate both free CO_2 and HCO_3-ions (see Österlind 1949).

In the total volume of water in the Inner Broad there is an annual average consumption of CO_2 of about 100 mg./litre because of the production of matter by the phytoplankton (photo-synthesis less respiration). Here the consumption of CO_2 by the photosynthesis of the attached

plants, which is by no means small, has been entirely disregarded. In the water of the Isefjord there is in all about 90 mg. CO_2 (total) per litre as CO_2 free, $CO_2\,HCO_3^-$, and $CO_2\,CO_3^{--}$. Therefore more CO_2 is used in a season than is found at any moment in the water-masses. Consequently considerable amounts of CO_2 must be supplied in the course of the year. This supply takes place partly from the bottom, as CO_2 is released by the bacterial decomposition of organic matter, partly from the large and small animals and bacteria living in the water, all these organisms through their respiration releasing CO_2, and partly by the uptake of CO_2 from the air. On the whole the supply of CO_2 must be so great that the water is not changed materially in respect of its content of the components of the carbon dioxide system. Thus in the late summers of 1941 and 1942 a pH of 8.2 was measured, which is entirely normal of sea water. Carbon dioxide does not become a minimum factor to the plankton algae in such an area as the Isefjord, as may happen in greatly eutrophic freshwater lakes with more or less the same content of $CO_{2\,(total)}$ at the beginning of the season as in the sea. A typical example is Søllerød Sø in Denmark (unpublished results).

Chapter Three

QUANTITATIVE INVESTIGATIONS OF PHYTOPLANKTON IN THE ISEFJORD

A. Survey.

In the preceding section there have been occasional references to the quantitative investigations of the phytoplankton in connexion with the discussion of the production of matter by the plankton. As for the Inner Broad, investigations have been made which cover the period from June 1940 to the end of August 1943. As for the Outer Broad and the area of the entrance to the fjord the material is scarce and is only intended as a supplement to the investigations in the Inner Broad. The plankton in the Roskilde Fjord has not been investigated at all.

The Utermöhl method was used at the investigations (Utermöhl 1931). An inverted microscope of the Leitz brand was used. Water samples from different depths were preserved with neutral formaldehyde (5 ml. 20 per cent. formaldehyde with 200 ml. sea water). For the same sample countings were made partly at a magnification of 100 times in a 10 ccm. tube chamber and partly at a magnification of 600 times in a special 2 ccm. chamber with a thin bottom. As a rule only each eighth stripe was counted at the highest magnification, so that only the plankton in 0.25 ml. was counted at this magnification. The samples from 1940 and 1941 were counted nearly immediately after being taken, while the samples from 1942 and 1943 generally were not counted until after about a year. This is generally of no importance as regards diatoms, Cyanophyceae, and most Peridineae, but it is of importance in the case of many flagellates. The number of flagellates, therefore, is generally stated only in the case of 1940 and 1941. On the whole the number of flagellates is rather problematic if preserved samples are used. A number of species, among them even such as are often of quantitative importance (e. g. *Prymnesium parvum*) disappear completely at a preservation. It seems to me that preservation with iodine gives no better results than preservation with neutral formalin in the case of marine species, as against Utermöhl's view in respect of the freshwater species.

Another difficulty as regards flagellates is due to the fact that in the case of the smallest species, particularly in a preserved state, it is almost impossible to determine whether the cells contain chlorophyll or not. By means of the determination of the production of matter it is in many cases possible to check the number of autotrophic flagellates. It is possible to determine e. g. that the predominant part of the photosynthesis at the end of June 1941 was due to the action of autotrophic flagellates. The amounts of diatoms, Peridineae, and Cyanophyceae were extraordinarily low. The number of flagellates was considerable according to the quantitative determinations (more than 200,000 per 100 ccm.). A considerable part must have been autotrophic. This could not have been decided with certainty if no determinations of the production of organic matter had been made.

Heterotrophic flagellates are often found in considerable quantities in the sea. Unfortunately time did not permit quantitative determinations of the living plankton. It is to be recommended in the case of quantitative investigations of plankton to undertake both centrifugation of living plankton and later counting of plankton preserved according to Utermöhl's method. Neither method is completely satisfactory in itself. Combined they must be said to be so. The combination has been used consistently in some investigations of the plankton in a Danish freshwater lake so far unpublished.

B. The Investigations of 1941.

We shall start with a discussion of the determinations in 1941, as the investigations in 1940 only cover the period June—October. Provisionally no consideration will be given here to the question which species of the various groups occur in the plankton at different times.

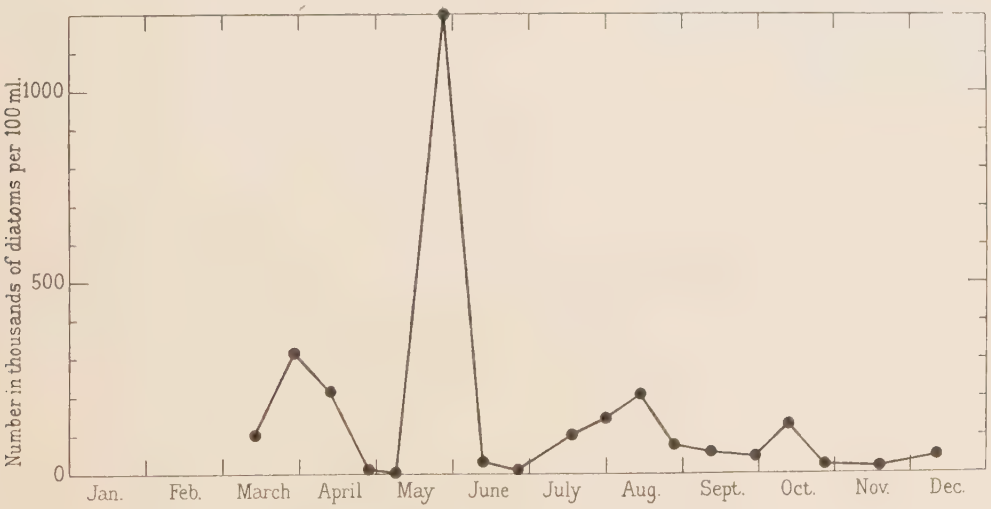


Fig. 21. Diatoms in the Inner Broad 1941.

The total number of diatoms (cells), Peridineae (cells), Cyanophyceae (colonies), and flagellates (cells) in the surface layer at the station in the Inner Broad in 1940 is represented graphically in figs. 21—24.

In 1941 the diatoms were generally the dominant group (fig. 21). The spring maximum of the phytoplankton, which set in as early as the beginning of March when the fjord was still ice-covered, was primarily due to diatoms. After the spring maximum the diatoms disappeared

nearly completely from the plankton. In the latter half of April and the former half of May there were practically no diatoms to be found. By the end of May there were again a very great population of diatoms. In the course of June the diatoms again disappeared almost completely, but in July a very high maximum of diatoms set in, with its peak in the middle of August.

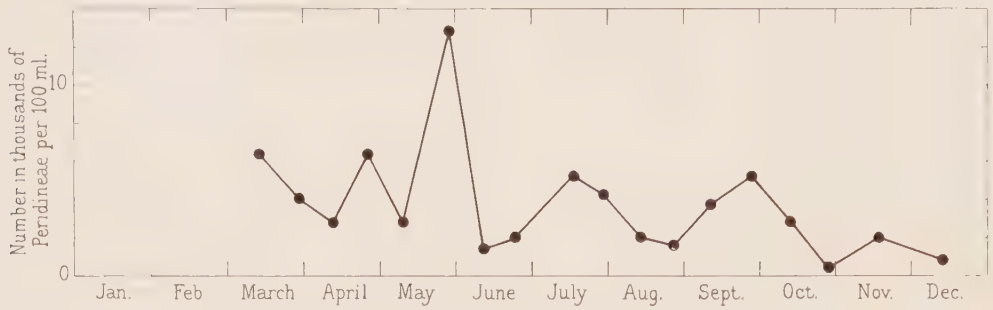


Fig. 22. Peridineae in the Inner Broad 1941.

This maximum largely, although with a falling tendency, lasted the rest of the year, the amount, however, having been materially reduced by September, while in the middle of October the curve of diatoms had a new peak.

During the whole of 1941 the Peridineae constituted a small part of the phytoplankton (fig. 22). On the whole the curve for the Peridineae follows neither the curve of the diatoms or that of the production of matter. The greatest number of Peridineae was, however, found at the end of May when also the greatest number of diatoms was demonstrated.

Practically no Cyanophyceae were found in 1941 (fig. 23). Flagellates were found all the year round, although in varying quantities (fig. 24). The two maxima were found at times when diatoms occurred in very small numbers, i. e. in the beginning of May and in June. As pointed out above, the determinations of the production of matter shows a large population of autrotrophic flagellates in June. The same is the case of the maximum of flagellates at the beginning of May, as the size of the production of matter at that time could not otherwise be explained.

Thus the different groups of organisms are by no means parallel in respect of their quantitative occurrence. The content of silica is of importance for the production of diatoms, but this substance is not necessary for the Peridineae and the flagellates. It has been shown several

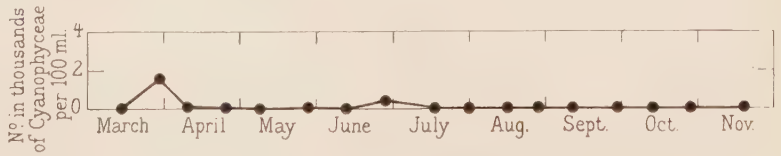


Fig. 23. Cyanophyceae in the Inner Broad 1941.

times that silica may be at a minimum. Thus Wattenberg and Meyer 1936 showed that this substance for periods in summer nearly completely disappeared from the surface layer in the Kiel Bay (less than 10 mg. Si/m.^{3}), while at other times concentrations of about 1000 mg. Si/m.^{3} were found at the surface. Determinations of silica were also made in the Isefjord in the period of August 1941—September 1942. Unfortunately the bottles used for collection of the samples contrary to expectation disengaged some silica. In winter up to 800 mg. Si/m.^{3} was detected at

the bottom and 600 mg. in the surface layer. The rest of the year amounts of about 150—400 mg. Si/m.^{3} were found. Even though these determinations do not give the real values of Si, which is lower than the values found, they show that silica was never present in quite so great quantities as e. g. in the Kiel Bay and thus presumably, as there, gets at a minimum. It is true that the

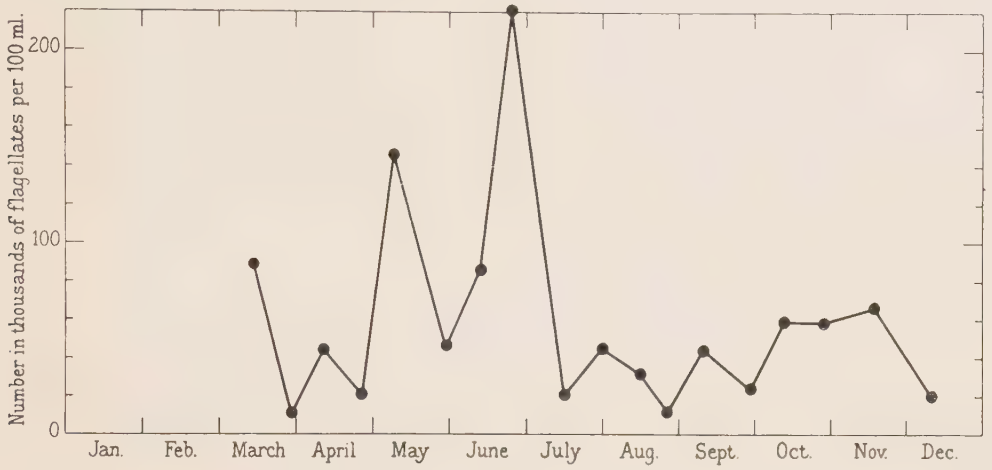


Fig. 24. Flagellates in the Inner Broad 1941.

depths are small in the Isefjord and further the volumes of water generally are not stabilized vertically. Simultaneously with the Si minimum in the surface layer considerable quantities of Si were found in the layer of water near the bottom in the Kiel Bay (about 1500 mg./m.^{3}). Considerable quantities are constantly dissolved from the bottom. In this way the volumes of water in the Isefjord must constantly be supplied with Si. There is, however, nothing remarkable in this, if the supply in the Isefjord cannot for periods keep up with the consumption of this substance and thus gets at a minimum.

The Isefjord cannot in that respect compare with conditions in the shallow brackish areas near Rügen (Gessner, 1937). In all these areas considerable quantities of Si were detected in all seasons (up to more than 3000 mg. Si/mg.^{3}). The supply of freshwater from the land carries large quantities of this substance with it there. Only in Hiddenseer-Bodden there was in April a "minimum" of 400 mg. Si/m.^{3}. During this "minimum" the content of Si, however, was nearly as large as the content of Si (600 mg./m.^{3}) found as a maximum in the Inner Broad of the Isefjord, a value which is even, as stated above, presumably somewhat too high.

C. The Investigations of 1942.

In 1942 as in 1941 the year started with an ice winter of long duration. The ice did not disappear from the Inner Broad until the beginning of April; but as early as March a considerable population of diatoms had developed immediately below the ice (fig. 25). Here there is no material vertical mixture of the water-masses, as appears from the vertical distribution of the diatoms: 68,000 immediately below the ice, 5,000 at a depth of 5 m. Only immediately below the ice the light is sufficient for a considerable production of autotrophic organisms. A similar vertical distribution is found in the case of the flagellates (9,000 immediately below the ice, 4,000 at a depth of 5 m.).

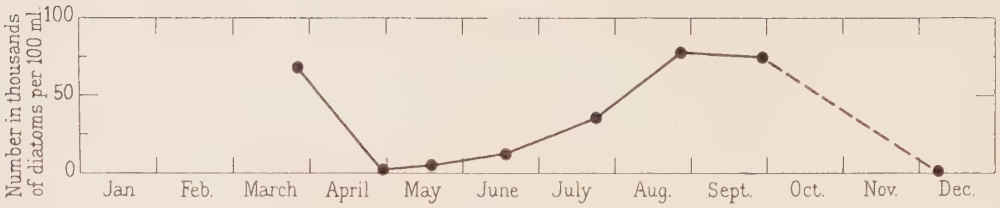


Fig. 25. Diatoms in the Inner Broad 1942.

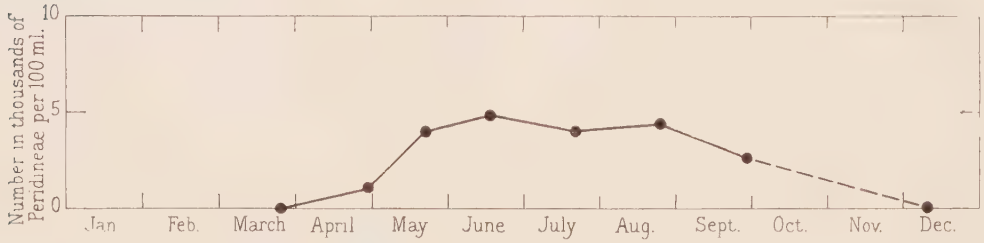


Fig. 26. Peridineae in the Inner Broad 1942.

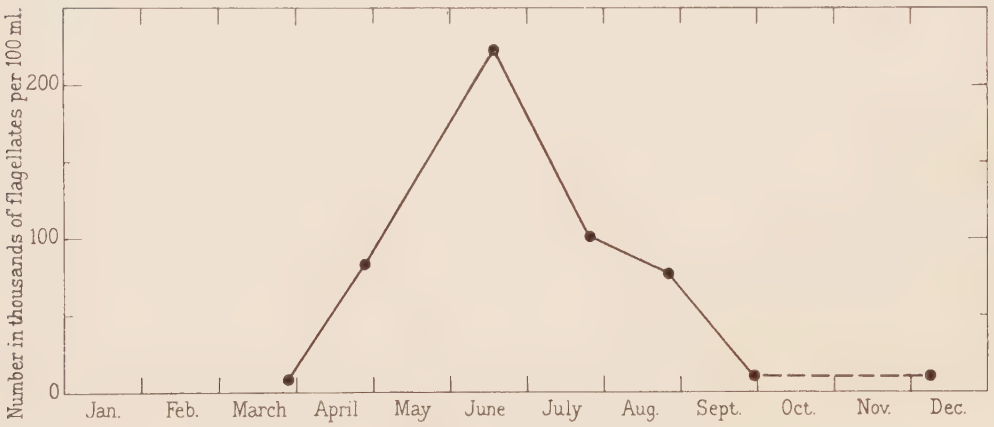


Fig. 27. Flagellates in the Inner Broad 1942.

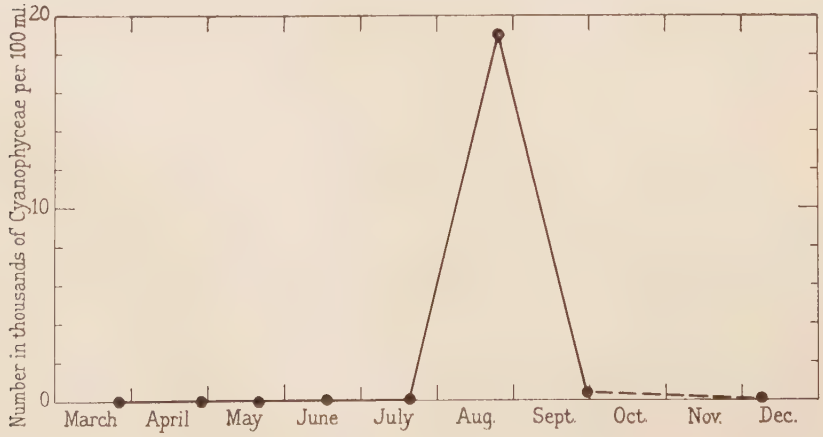


Fig. 28. Cyanophyceae in the Inner Broad 1942.

After the spring maximum of diatoms a distinct minimum started in April—May as in 1941. In June—July there was again an increase in the number of diatoms. This summer maximum had reached its peak in August—September. A high maximum of short duration similar to that at the end of May 1941 was not observed in 1942. Such a maximum may, however, have escaped our attention as collections of plankton were made only once a month.

The Peridineae (fig. 26) in 1942 showed a single maximum lasting from May to September. The Peridineae were present in small amounts as compared with the number of diatoms. The flagellates in 1942 (fig. 27) showed a single high maximum from April to August with its peak in June. The Cyanophyceae (fig. 28), which in 1941 were practically absent in the plankton, occurred at the end of August 1942 in the rather considerable number of 19,000 colonies per 100 ccm. Quite insignificant quantities were found at other times in 1942.

D. Investigations of 1943.

Because of the absence of an ice cover in 1943 the "spring maximum" of diatoms set in much earlier than in 1941 and 1942. It began at the end of January and had its peak in February (fig. 29).

In March the number of diatoms had decreased considerably, and in April they had disappeared completely from the plankton. A great number appeared again in May. The peak

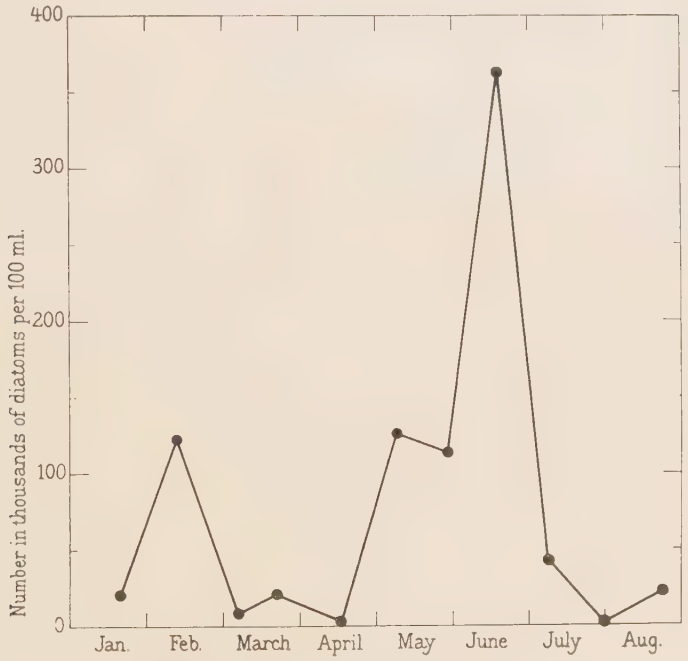


Fig. 29. Diatoms in the Inner Broad 1943.

of this maximum was in June. In July the number of diatoms decreased again. At the end of the month the diatoms had nearly completely disappeared from the plankton. In August the number of diatoms began to increase again. In this month the collection of plankton was discontinued.

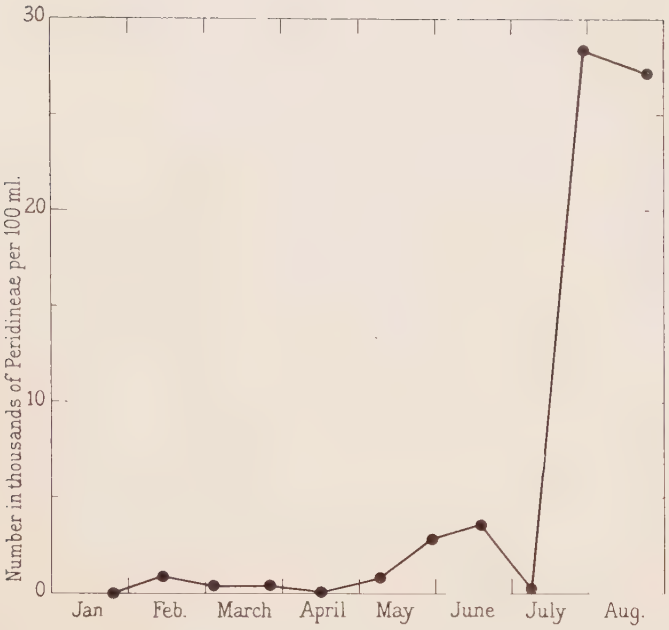


Fig. 30. Peridineae in the Inner Broad 1943.

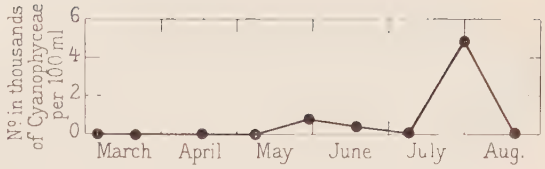


Fig. 31. Cyanophyceae in the Inner Broad 1943.

Peridineae (fig. 30) during the whole former half of 1943 were found in quite insignificant numbers. In May—June there was, however, a relative maximum. At the end of July and in August many Peridineae were found in the plankton, up to nearly 30,000 per 100 ccm. Quantities of Peridineae of that size were not found in any of the other years of investigation.

Cyanophyceae (fig. 31) were found from May in 1943. By the end of August they had, however, disappeared from the plankton. Their maximum was at the end of July, with 5,000 colonies per 100 ccm.

As stated on p. 44, it is not possible with certainty to give the number of flagellates in 1943. However, already in January a fair number of flagellates was found: at least 45,000 per 100 ccm. A very great number was found in the height of summer (July—August).

E. Investigations of 1940.

In the period of June—October four excursions were made through the fjord. The innermost station (III) was situated at the same place as the station in the Inner Broad 1941—1943. Station II was in the middle of the Outer Broad and Station I was in the entrance area immediately north of the harbour of Hundested (see chart fig. 1 p. 8).

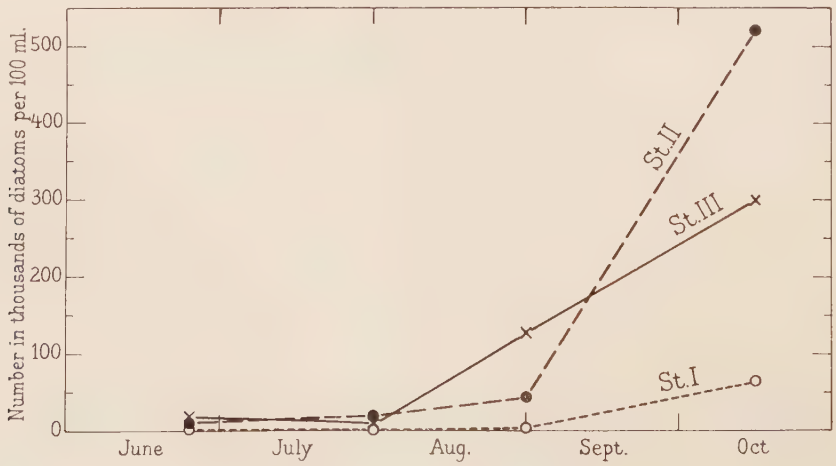


Fig. 32. Diatoms in the Isefjord 1940.

Fig. 32 shows the number of diatoms in the surface layer on the various excursions and at the various stations. At St. III comparatively small numbers of diatoms were present at the end of June and on the 1st of August. By the end of August the number had increased

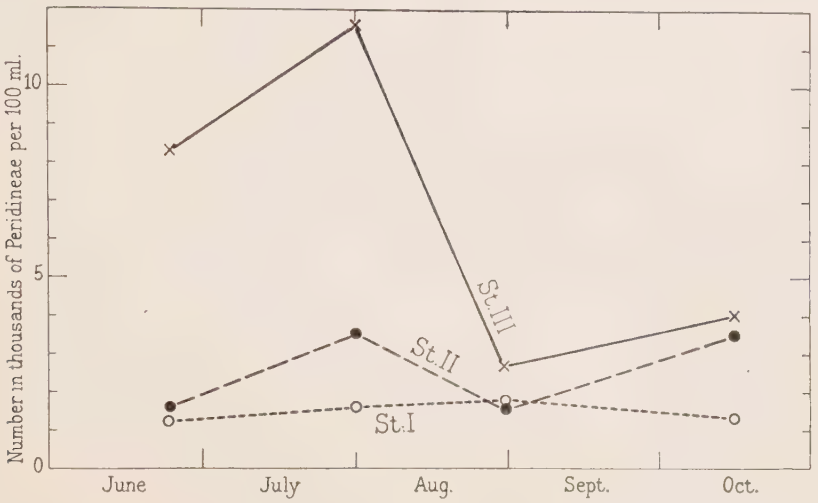


Fig. 33. Peridineae in the Isefjord 1940.

considerably (125,000 per 100 ccm.). In October the number of diatoms had increased further to 300,000 per 100 ccm.

Very similar conditions were found at St. II in the Outer Broad, whereas quite insignificant numbers of diatoms were found throughout the summer at St. I in the entrance area. In October a maximum was found there, though much smaller than at the stations in the fjord proper.

Peridineae (fig. 33) were found in the surface layer at St. III in comparatively small

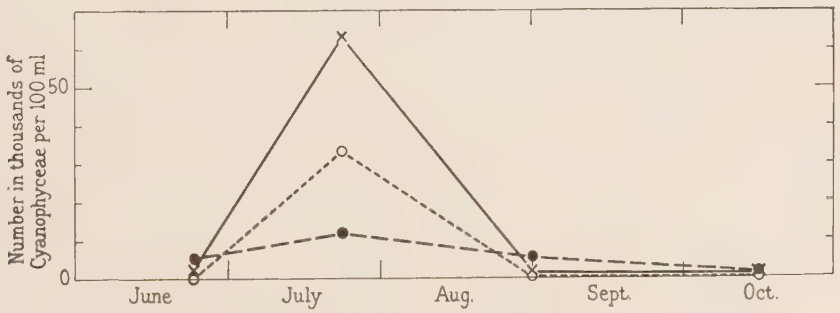


Fig. 34. Cyanophyceae in the Isefjord 1940.

quantities in June and August. Otherwise only fair quantities of these organisms were found. The same was the case of Stations II and I.

On the excursion on August 1st considerable quantities of Cyanophyceae were found at all the three stations (see fig. 34). Cyanophyceae were also as a rule found on the other excursions, but only in small quantities (signatures as in fig. 33).

A very large number of flagellates (fig. 35) was found at Station III on June 24th (more than a million per 100 ccm.). Considerable quantities of flagellates were also found on the other excursions in the height of summer. In October the number had decreased to 35,000 per 100 ccm.

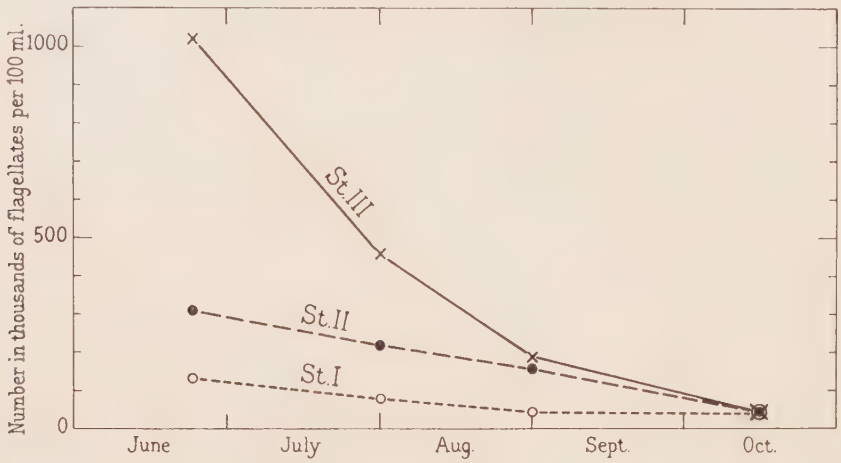


Fig. 35. Flagellates in the Isefjord 1940.

In principle St. II showed the same conditions as St. III, although the quantities were generally somewhat smaller. This still more applies to St. I.

As a rule the vertical distribution of the plankton has not been considered in the survey of the plankton in the Inner Broad in the various years. The vertical mixture of the water-masses is generally so great there that the phytoplankton gets an even vertical distribution. The plankton was, however, always counted both in the surface layer and near the bottom. As an example fig. 36 shows the number of diatoms per 100 ccm. in 1940 at St. III (the Inner Broad) both in the surface layer and near the bottom (at a depth of 5 m.). At the station in the entrance to the fjord (St. I), the water at the surface and at the bottom, however, are often of different origin, which shows itself in different plankton, particularly in a quantitative respect (see fig. 37), but sometimes qualitatively as well. On June 24th, 1940, the salinity was 16.4 $^0/_{00}$ in the surface layer and 19.0 $^0/_{00}$ at a depth of 6 m. In the surface layer there were e. g. 2,800 diatoms per 100 ccm. The dominant species was *Thalassiosira nana* (1,600 per 100 ccm.). At a depth of 6 m. there were 11,000 diatoms with *Sceletonema costatum*, which was not found in the surface layer, as dominant species (4,600 per 110 ccm.), whereas *Thalassiosira* was not observed at all at a depth of 6 m.

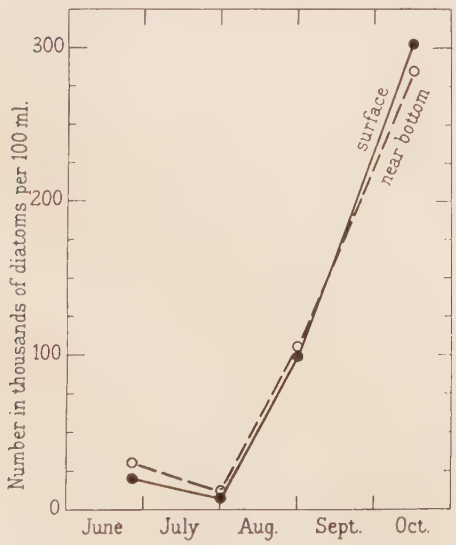


Fig. 36. Diatoms at the surface and at a depth of 5 m. in the Inner Broad 1940.

In the Outer Broad there may be a great difference between the plankton in the surface layer and that farther down in periods of calm weather, when the water-masses are stabilized because of greater heating in the surface layer. The differences, however, are mainly quantitative, not qualitative. Fig. 38 shows the vertical distribution of

the various groups of organisms on June 24th, 1940. It is clearly seen that at a depth of 8 m. there are considerably greater quantities than in the surface layer and at a depth of 4 m.

The water-masses were very transparent during that period. At a depth of 8 m. the inten-

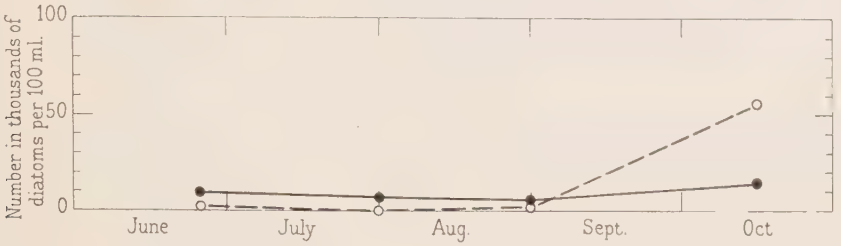


Fig. 37. Diatoms at the surface and at a depth of 6 m. in the entrance area 1940. ●——● surface, o---o near bottom.

sity of the green light had dropped to one fourth of that immediately below the surface (see p. 26). As at the same time a considerable quantity of phosphate was present at this depth (15 mg. P/m.^{3}), while only 3 and 0 mg. P/m.^{3}, respectively, were detected in the surface layer and at a depth of 4 m., conditions of production must be best at a depth of 8 m. The larger quantities of phytoplankton at this depth thus seem very natural. The poor saturation with oxygen at a depth of 8 m. (66 per cent.), indeed, does not indicate any appreciable photosynthetic activity, since oxygen develops by this process, for which reason we should expect a supersaturation with oxygen instead of undersaturation. However, the undersaturation may presumably be explained by the proximity to the bottom, which was at a depth of 9.5. At the bottom there is a very considerable consumption of oxygen because of bacterial decomposition of organic matter.

The plankton material of 1940 does not give quite a sufficient basis for a comparison between the Inner and the Outer Broad. As to the phytoplankton there does not, however, seem to be any material difference in a quantitative respect between the two areas, even though the Outer Broad may be a little poorer than the Inner Broad. Qualitatively the plankton in the two areas is in full agreement. The entrance area, which forms the transition between the Kattegat and the Isefjord, cannot, as regards plankton, be considered a separate area. This is particularly the case in summer, when conditions of production by the phytoplankton in the Isefjord and the part of the Kattegat situated immediately outside the fjord are of quite different characters, as at that time there are optimum conditions of production in the former place, but rather poor conditions in the latter. On the whole the plankton is in summer quanti-

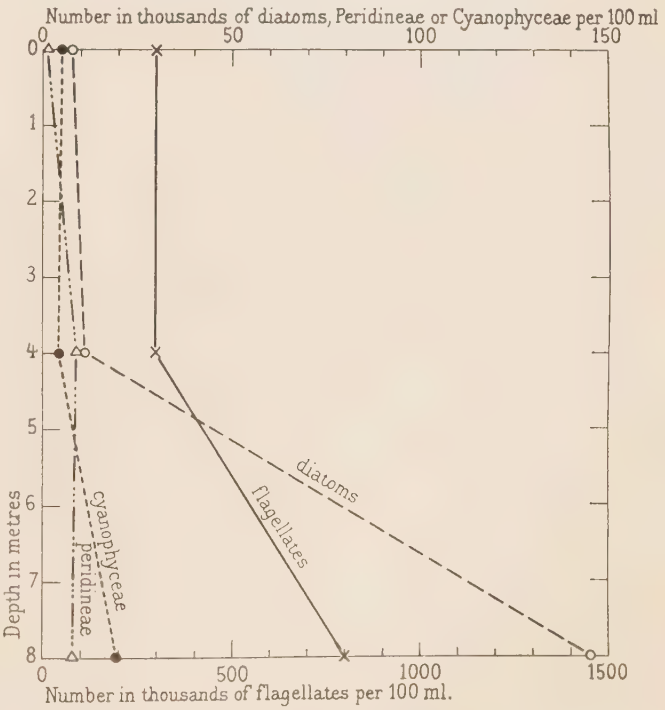


Fig. 38. Vertical distribution of plankton in the Outer Broad 24.6.1940.

tatively much poorer in the entrance area of the fjord than in the fjord proper. Because of the exchange of water between the fjord and the southern Kattegat we shall in the entrance area, when longer periods are considered, be able to find all species found either in the fjord or in the southern Kattegat. Further particulars about this question will be given in Chapter Four, where the floristics of the plankton is treated.

F. Comparison between the Stocks of Phytoplankton of the Various Years 1940—1943.

As we have seen above, conditions of production of the phytoplankton in the Inner Broad in 1941 and 1942 were in agreement. In 1943 the production set in much earlier, as no ice delayed the spring maximum in this year. The spring maximum, however, in all years was primarily based on diatoms, even though, as we shall see in Chapter Four, the composition of species varied somewhat in 1943, when the typical "ice species" *Detonula confervacea* was not found.

After the spring maximum comes a poor plankton in respect of all groups of organisms. Considerable quantities of phytoplankton are not produced again until May. This summer maximum lasts the whole of the summer and the greater part of the autumn. The composition of the plankton, however, varies greatly. The diatoms, which during periods of the summer-autumn maximum were the dominant organisms in all the years of investigation, culminated at various times in the various years. In 1940 the diatoms culminated in the autumn: no appreciable quantities of them were present in the plankton until the end of August. In 1941 there was partly a maximum of diatoms at the end of May and partly a maximum in July—October with an absolute maximum by the middle of October. In 1942 there were also rather large quantities of diatoms in the period July—October. The amount of diatoms was, however, considerably less in 1942 than in 1941 (cp. fig. 21 with fig. 25). In 1943 relatively large quantities of diatoms were found in May and June, but these organisms had disappeared nearly completely from the plankton about August 1st.

Considerable amounts of flagellates are found during the summer-autumn maximum of the plankton. The amounts were largest in June—July in all years. In June 1940 the absolutely largest amounts were found: more than 1 million cells per 100 ccm.

As regards the Cyanophyceae there was a difference between the various years. In 1940 there was a distinct maximum about August 1st. In 1941 there were practically no Cyanophyceae in the plankton. In 1942 a rather considerable maximum was found at the end of August, while in 1943 small amounts of Cyanophyceae appeared about July 1st. It is seen that the Cyanophyceae, if they do develop in the plankton in the Isefjord, make their appearance in the warmest time of the year. The absence of Cyanophyceae from the plankton in 1941 is not due to a cold summer, since, on the contrary, the temperature in July—August of that year was relatively high in the Isefjord.

Chapter Four

THE MAIN SPECIES OF PHYTOPLANKTON IN THE ISEFJORD

A. Survey.

Ostenfeld, 1913, has given an excellent survey of the distribution in the Danish waters of the species of phytoplankton which are detained by fine-meshed silk nets. Thorough investigations of smaller species which will pass through the meshes of the silk are still missing. This especially applies to the group of the flagellates. It is generally impossible to determine these in a preserved state, if indeed they can be preserved at all. As to the distribution of the chief small diatoms and Peridineae in the Danish waters in the various seasons reference may be made to the tables in Steemann Nielsen, 1940.

The investigations in the Isefjord suffer from the defect that the plankton was examined in a preserved state. In this state a number of organisms, particularly flagellates, cannot be determined as to species. For practical reasons this method was necessary. However, there is no doubt that investigations of living plankton combined with cultivation experiments might have produced important results. It is to be hoped that such work will be taken up, not only in the case of the Isefjord, but of the Danish waters in general.

Information about at any rate the main species of the fjord will be given in what follows. Very scarce large species the occurrence of which in the net plankton can easily be shown, will only be observed by accident if Utermöhl's method is used. For production investigations such as the present ones the inclusion of such species is without any material importance.

B. Diatoms.

Thalassiosira nana Lohm.

This small species is found in the open Danish waters all the year round. In the Kattegat with the exception of the very southernmost part it was generally scarce in 1935—36, whereas it was among the dominant species in the Baltic both in the early spring (March—April) and in the height of summer, which shows that it is a eurythermal species (Steemann Nielsen, 1940).

In the Isefjord it was in 1940 found at all times of investigation (i. e. June—October) with its maximum at the end of August (about 10,000 per 100 ccm.). In 1941 it was only found in July (up to about 9,000 per 100 ccm.). In 1942 it was found only in June—August with its maximum in June (about 8,000 per 100 ccm.). In 1943 this species was not observed in the Isefjord. As distinct from conditions in the open Danish waters *Thalassiosira nana* thus in the Isefjord was found only in the warmest months of the year.

Thalassiosira Nordenskjöldii Cleve.

As shown by Ostenfeld this species is found in the Danish waters only in the coldest months of the year. This also applies to the Isefjord, where, however, it played no quantitative part. The greatest number was found on April 9th, 1941 (1,600 per 100 ccm.).

Thalassiosira gravida Cleve.

The occurrence of this species in the Isefjord is like that of *T. Nordenskjöldii.*

Sceletonema costatum (Grev.) Cleve.

This species is one of the most important producers of organic matter in the Isefjord. Figs. 39—42 shows the quantitative conditions of the species in the Inner Broad during the years 1940—1943. In 1941 and 1943 *Sceletonema* was the dominant organism during the spring maximum, while in 1942 it was not observed at all at that time. In this year the species had only a minor maximum in July, while outside this period it was totally absent from the plankton. In 1940 considerable quantities of *Sceletonema* were present both at the end of August and in the middle of October. In 1941, besides the spring maximum of *Sceletonema* at the end of March, a very high maximum was found at the end of May, with more than a million cells per 100 ccm. In this year the species was present in the plankton throughout the height of summer, although in moderate quantities only. After an absolute maximum in September—October a fresh maximum was observed in November—December (well over 40,000 cells per 100 ccm. in the middle of December).

Fig. 39. *Sceletonema* in the Inner Broad 1940.

In 1943, when the spring maximum of the plankton set in very early because of the absence of an ice cover, large amounts of *Sceletonema* were found in January—February (more

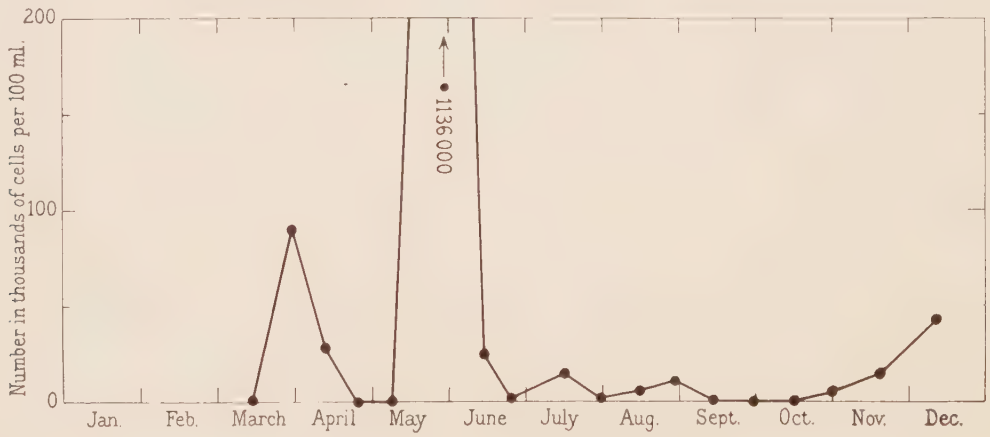


Fig. 40. *Sceletonema* in the Inner Broad 1941.

than 100,000 cells per 100 ccm. in the former half of February). Another considerable maximum was found in May (up to well over 60,000 cells per 100 ccm.). In the height of summer of this year the species was generally present in the plankton although in very moderate quantities.

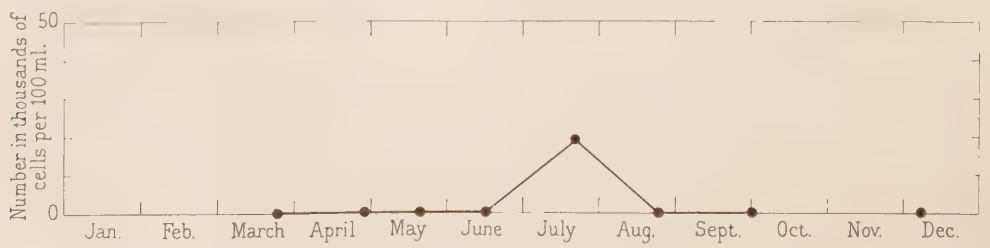


Fig. 41. *Sceletonema* in the Inner Broad 1942.

Sceletonema is found both in the plankton and as a bottom species, it being found as the dominant species at the bottom of the Isefjord at any rate in the height of summer and the autumn, the only times at which investigations of this vegetation were made in the fjord. The investigations show that large amounts of the species can be found in the plankton at all times of the year.

In his summary survey of the occurrence of the species in the plankton of the open Danish waters OSTENFELD 1913 says that *Sceletonema* has a distinct maximum in the early spring (about March), but in some years this may be completely or partly suppressed. Besides this maximum there may be a secondary maximum in the autumn, but at greatly varying times. The investigations in the inner Danish water in 1935—1936 (STEEMANN NIELSEN, 1940) quite corroborated OSTENFELD's observations. It should, however, be mentioned that a maximum of *Sceletonema costatum* was found in the Sound in June 1933 besides the normal spring maximum in March (STEEMANN NIELSEN, 1937).

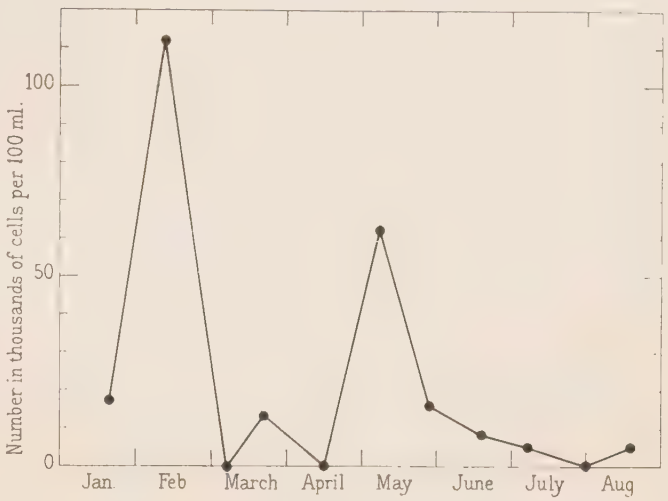


Fig. 42. *Sceletonema* in the Inner Broad 1943.

OSTENFELD showed that *Sceletonema* in the Limfjord behaved in another way than in the open waters, as there was generally a minor maximum in the height of summer besides the spring maximum. In 1900 *Sceletonema* was practically completely absent from the plankton in the Limfjord with the exception of an insignificant maximum in July. This corresponds to conditions in the Isefjord 1942. OSTENFELD, as a possible cause of the absence of the spring maximum in the Limfjord in 1900, mentions the fact that in November—December 1899 there was a considerable maximum of the species. This maximum thus would correspond to the maximum which ought to have appeared in the spring of 1900. It is interesting that apparently conditions can be quite the same in the Isefjord, as in November—December 1941 there was a considerable maximum of *Sceletonema*, while the spring maximum to be expected in March 1942 failed to appear. At any rate this is not to be explained by the nutrients to be used at the normal spring maximum of *Sceletonema* having already been used during the maximum in November—December. The mere occurrence of a normal spring maximum in March, only consisting of other species, goes against this. On the other hand we cannot ignore the fact that inner factors in the diatoms themselves may assert themselves, so that a maximum exhausted November—December can prevent the appearance of a normal spring maximum the next year. As to the inner factor determining the rhythm of a plankton species in nature we are still nearly completely ignorant.

Detonula confervacea (Cleve) Gran.

According to OSTENFELD, 1913, *Detonula confervacea* in the Danish waters is only endogenous in the Limfjord (the only fjord that was investigated). A considerable amount was found here in the earliest spring.

In the Isefjord the species behaves exactly as in the Limfjord. Both in 1941 and 1942 considerable amounts had developed under the ice at the end of the ice season. In 1943, when the fjord was not frozen over, *Detonula confervacea* was not observed in the plankton.

In 1941 the species was present at any rate from the first half of March to the end of April, but already in the beginning of April the species had developed resting spores, near the end of April only resting spores were observed. The peak of the maximum was found at the end of March (nearly 200,000 cells per 100 ccm.).

The appearance of *Detonula* in the Limfjord would seem to indicate that it only occurs in the plankton in the years when the ice covers the fjord. This is not corroborated by Ostenfeld's investigations from the Limfjord, as in March 1899 the species was prominent although there was no real ice cover.

Leptocylindrus danicus Cleve.

The species was observed in 1940, 1941, and 1942 in the months of June—October. Generally it was only present in a number of at most 3,000 per 100 ccm. However, 13,000 per 100 ccm were found in the beginning of October 1941.

Leptocylindrus minimus Gran.

This small species, which passes through the meshes of the fine-meshed silk net, was not found in Ostenfeld's investigations in the Danish waters. At the investigations in 1935 and 1936 (Steemann Nielsen, 1940) it was generally found in the company of *Leptocylindrus danicus,* but only in smaller amounts, so that it is not included in the lists of quantitatively significant organisms. It has previously been found in the Kieler Förde as well. In the Isefjord it was also found as a companion of *Leptocylindrus danicus.* It was found in all the four years of investigation, generally in the time from the end of May to November. In 1942, however, it was observed only in June. The greatest number of the species was found at the end of August 1940 (6,000 per 100 ccm.). On the whole small amounts of *Leptocylindrus minimus* were present.

Guinardia flaccida (Castr.) Perag.

According to Ostenfeld this species is widely distributed in the Danish waters and plays a fairly considerable part there. The first part of this statement is absolutely correct, whereas the second part is somewhat problematic. Because of its size it is much more easily caught in silk nets than most other diatoms, so in the case of net investigations we get a somewhat incorrectly drawn picture of the quantitative importance of the species. At my quantitative investigations in the Danish waters in 1935 and 1936, at which Utermöhl's sedimentation method was used, *Guinardia flaccida* was never present in so great quantities that it was included in the lists of the quantitatively important species. The same was the case of the investigations in the northern part of the Sound in 1932—1933.

In the Isefjord itself *Guinardia flaccida* was observed only once in June 1941. In the entrance area it was further present in October 1940. The species does not seem really to belong to the Danish fjords. According to Ostenfeld very small quantities of the species were found in 1897—1901 in the Limfjord, "where it probably occurs only as an immigrant through Tyborøn Kanal".

Rhizosolenia alata Brightw.

In the Kattegat *Rhizosolenia alata* is one of the predominant species in summer and in the autumn. In the rest of the year only small quantities of it are found. According to Ostenfeld 1913 it was not found in March and April, but so it was at the investigations in this area in 1935 and 1936 (see Steemann Nielsen, 1944, fig. 11, p. 33). According to Ostenfeld the species in most years is completely absent from the Limfjord. The very few findings there are presumably due to accidental conveyance by the current. *Rhizosolenia alata* is no particularly conspicuous species in the Isefjord either. Still it has been observed in all years of investigation, particularly in the height of summer. A single finding dates from April (1943). At the end of June 1940 more than 7,000 per 100 ccm. were found at a depth of 5 m. in the Inner Broad; in July 1942 2,400 (auxospore formation) per 100 ccm. Otherwise very few cells were observed.

Rhizosolenia fragillima (Bergon) Gran.

This species was found in the warm season of 1940, 1941, and 1942. Quantitatively it was generally without any significance at all. In September 1941, however, about 3,000 cells per 100 ccm. were found.

Rhizosolenia Shrubsolei Cleve.

In the North Sea the species is found in all seasons. According to Ostenfeld it is allogenetic in the waters within the Skaw. It will only exceptionally reach the southern part of the Kattegat.

Small quantities of it were found in the Isefjord in February and March 1943.

Rhizosolenia setigera Brightw.

This species was observed in the Isefjord in all the years of investigation except 1942. It is generally without quantitative significance. A maximum (about 6,000 per 100 ccm). was found in the middle of July 1941.

Rhizosolenia styliformis Brigthw.

This oceanic plankton diatom according to Ostenfeld 1913 does not reach the southern part of the Kattegat. A few specimens were, however, found in the Isefjord in December 1941.

Rhizosolenia hebetata Bail.

A great number of specimens of the forma *semispina* (Hensen) Gran of this species occur in the Kattegat in the coldest season of certain years (Ostenfeld, 1913). In 1935 and 1936 it was, however, without any quantitative significance whatever. In the Inner Broad of the Isefjord moderate quantities of it (up to more than 4,000 per 100 ccm.) were found in Februar—March 1943. Otherwise few examples were found in the middle of October 1940 in the Inner Broad and in the entrance area.

The Chaetoceros Species.

Many species of the genus *Chaetoceros*—especially the small ones—are often difficult to determine, particularly when they are kept in counting chambers where they settle in a way in which important characters are not visible. At the countings it has often been necessary

to merge a considerable amount of the *Chaetoceros* population in a general group. Therefore the following survey of the occurrence of the *Chaetoceros* species in the Isefjord is not adequate. On May 28th, 1941, there was thus a population of more than 100,000 cells per 100 ccm. which could not be specified. As a whole the genus *Chaetoceros* plays a considerable part in the plankton of the fjord both in spring, summer, and autumn.

Chaetoceros danicus Cleve.

This species, which is easily recognized in counting chambers, has not been found in the Isefjord in the years of investigation. The salinity of the fjord is presumably too high for this diatom, which belongs to the Baltic.

Chaetoceros decipiens Cleve.

This species is also easily recognized. Quite an insignificant amount was observed in the Isefjord from April to June.

Chaetoceros compressus Lauder.

In the Kattegat great amounts of this species can be found in practically all seasons. A considerable number (on July 30th, 1941 more than about 50,000 per 100 ccm.) was found in the Isefjord in the summer months (June—September) of 1940 and 1941.

Chaetoceros affinis Lauder.

The species is found in the fjord in summer without being quantitatively of any importance whatever.

Chaetoceros brevis Schütt.

As *C. affinis*.

Chaetoceros similis Cleve.

The occurrence of this species in the Isefjord in June and November 1941 was ascertained.

Chaetoceros subtilis Cleve.

This species was found in April 1941, May 1943, and August 1940, in the two cases first mentioned in considerable amounts (in April 1941 more than 10,000 per 100 ccm.).

Chaetoceros curvisetus Cleve.

A number of more than 8,000 cells per 100 ccm. of this species characteristic of the warm season in the Danish waters was found in the middle of July 1941. In the middle of October 1940 a smaller amount of the species was present everywhere in the fjord.

Chaetoceros debilis Cleve.

Rather considerable amounts of this species (on April 9th, 1941, more than 40,000 cells per 100 ccm.) were found at the beginning of April and in September—October 1941. In the other years of investigation *Chaetoceros debilis* was without any importance at all.

Chaetoceros radians Schütt.

At the end of August 1940 small amounts of this species were found both in the Inner and the Outer Broad.

Chaetoceros simplex Ostenfeld.

According to Ostenfeld this small *Chaetoceros* species, which does not form chains, is characteristic of fjords and similar localities in summer. This statement is corroborated by the appearance of the species in the Isefjord. It was found in summer in all the years of investigation, often in considerable quantities, in July 1941 thus in a number of about 50,000 per 100 ccm.

Chaetoceros ceratosporus Ostenfeld.

Without resting spores this species is rather difficult to distinguish from the preceding species. It is, however, a cold-water species. It was found with spores at the beginning of April 1941. It was also present at the end of March of the same year (2,000 per 100 ccm.). A few individuals probably also belonging to this species were found in December 1941.

Cerataulina Bergonii H. Perag.

This is one of the quantitatively important plankton algae in the Isefjord, as also in the Kattegat. It was found in all the years of investigation. In 1941 and 1942 it began to appear in June, in 1943 already from the beginning of May. In the middle of November 1941 it was still present. The greatest amount was counted in June 1943 (more than 300,000 per 100 ccm.), but great amounts of the species were also found in periods in the summer or the autumn of the other years.

Asterionella japonica Cleve & Möller.

According to Ostenfeld 1913 this species only to quite a small extent penetrates into the Danish waters within the Skaw. At the investigations 1899—1901 it was not observed farther

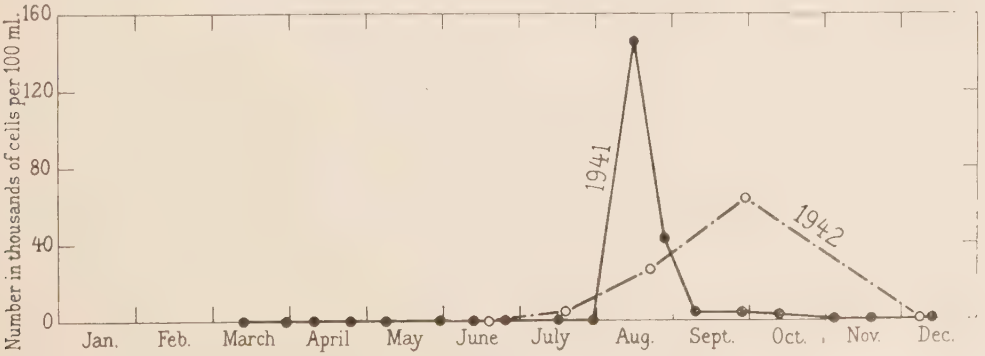


Fig. 43. *Asterionella* in the Inner Broad 1941 and 1942.

south than near Læsø, where it was very rare. At the investigations in 1935 and 1936 (Steemann Nielsen, 1940) considerable amounts of the species were present in the northern and middle part of the Kattegat in the autumn. Farther south in the Kattegat only a very few specimens were found.

Therefore it was rather astonishing that *Asterionella japonica* in the Isefjord both in 1941 and 1942 developed high maxima in August and September, respectively (see fig. 43). Net samples taken twice a month during the whole of 1941 in the southern part of the Kattegat (Schultz Grund lightship) were examined without one specimen being found. In 1940 and 1943 *Asterionella japonica* was not observed in the Isefjord.

Fragilaria minima Steemann Nielsen.

Small quantities of this very small diatom, originally described from the continental shelf area in the northern Atlantic, were found in the Isefjord in September 1941 and in April 1942.

Thalassiothrix Nitschioides Grun.

According to Ostenfeld this species occurs in the Danish waters outside the Baltic in all seasons, developing maxima proper in the cold season. In the Limfjord it developed, however, a maximum in July 1897. Similarly *Thalassiothrix Nitschioides* in August 1940 showed a high maximum in the Isefjord (in the Inner Broad about 55,000 per 100 ccm. on August 30th, 1940). At all seasons of the years of investigation 1940—1943 the species was observed in the Isefjord. With the exception of the maximum mentioned above only small quantities of the species were present (in April 1943, however, about 3,000 per 100 ccm.).

Achnantes taeniata Grun.

Considerable quantities of this species were observed in March and April 1941 (21,000 per 100 ccm on March 28th, 1941). Otherwise this diatom was not found in the Isefjord. In the inner Danish waters Ostenfeld found *Achnantes taeniata* only in the Limfjord (March 1897). Although the salinity in the Limfjord is about 10 $^{0}/_{00}$ higher than in the Isefjord, the two fjords show a considerable similarity as regards the occurrence of species which generally are not found in the Danish waters. Another typical example was *Detonula confervacea* mentioned above.

Nitzschia seriata Cleve.

In 1899—1901 *Nitzschia seriata* according to Ostenfeld was very rare in the Danish waters. For instance, it was not observed in the southern Kattegat (Schultz Grund lightship). In 1935 and 1936 the species was found in the whole of the Kattegat, in the Great Belt, and in the northern part of the Sound with the exception of the height of summer.

In the Isefjord about 6,000 per 100 ccm. were found in October 1940, about 1,000 per 100 ccm. in September 1941, and up to 3,000 per 100 ccm. in January—March 1943.

Nitzschia delicatissima Cleve.

This is one of the dominant species of the Kattegat in the cold season. At any rate such was the case in 1935 and 1936 (Steemann Nielsen, 1944). The fact that Ostenfeld 1913 did not find the species in the Kattegat is due to the species being so small that it will pass through the meshes of the silk nets.

In the Isefjord only small and scattered quantities of *Nitzschia delicatissima* were found in 1940—1942. In 1943 there was a distinct maximum from January to June with its peak in May (about 40,000 per 100 ccm.).

Nitzschia closterium (Ehrbg.).

This small diatom, which is also found as a bottom form, was observed in all the years 1940—1943. In 1941 it was found in practically all samples from the end of March to November, although generally in small amounts (still, more than 6,000 in the middle of July). In 1942 it was only found in August—September, but with a considerable maximum at the end of August (11,000 per 100 ccm.). In 1943 small quantities were found from March to July.

Bacillaria paradoxa Gmel., van Heurck.

To my knowledge this characteristic species, which is also caught in the fine-meshed silk nets, has never before been observed in the inner Danish waters. It is found in the North Sea. Small numbers of it were found in the Isefjord in August and October 1941.

Bottom Diatoms in the Plankton.

In such a shallow area as the Isefjord a number of bottom species are often found in the plankton. They do not play any quantitative part here, apart from the species which, like *Sceletonema costatum*, may also appear as typical plankton species. To this category also belong: *Grammatophora serpentina* Kütz. and *Biddulphia aurita* (Lyngb.), of which a small amount was found in the plankton in March 1941, and *Paralia sulcata* (Ehr.) Cleve, which was found in small amounts scattered over the whole time of investigation.

C. Peridineae.

Exuviaella baltica Lohm.

With the exception of the period July—September this small species was nearly always present in the plankton in the Isefjord in 1940—1943. This is in agreement with conditions in the Kattegat in 1935 and 1936 (see Tables 5—14, Steemann Nielsen, 1940). Only small quantities were found in the Isefjord (greatest amount 1,600 per 100 ccm. on June 16th, 1942).

Prorocentrum micans Ehrbg.

In contrast to the preceding species *Prorocentrum micans* was found in the Isefjord in June—November. Only on August 1st, 1940, it was found in considerable quantities (about 3,000 per 100 ccm.); but it was observed regularly in all the years of investigation.

The family Gymnodiniidae.

The species within this large and important family generally cannot be determined as to species in a preserved state. Species of both the genus *Amphidinium* and the genus *Gymnodinium* are common in the Isefjord. They occurred in practically all samples from all years of investigation. The greatest quantities occurred in June and August 1940 (about 10,000 per 100 ccm.), in May 1941 (about 9,000 per 100 ccm.), and in July 1943 (about 10,000 per 100 ccm.).

Dinophysis norvegica Clap. & Lachm.

Observed once (June 16th, 1942).

Dinophysis acuminata Clap. & Lachm.

Observed in August and December 1941.

Glenodinium sp.

A very small amount of a small *Peridinea* presumably belonging to the genus *Glenodinium* was found from April to September.

Protoceratium reticulatum (Clap. & Lachm.) Bütschli.

Small amounts of this species were found in the height of summer in 1940, 1941, and 1942.

Peridinium triquetrum (Stein) Lebour.

Large amounts of this species were found in the Isefjord in July and August 1943 (about 20,000 per 100 ccm.). Otherwise very small quantities were found and only in the summer months.

Peridinium trochoideum (Stein) Lemm.

Small amounts of this species were found in the Isefjord in May 1943.

Peridinium divergens Ehrbg.

The species was found in the summer months of 1940, 1941, and 1942, but always in quite small quantities.

Peridinium pellucidum (Bergh) Schütt.

Insignificant quantities of this species were found from April to October 1941.

Minuscula bipes (Paulsen) Lebour.

Small quantities of this small species were found in the summer and autumn months of 1940 and 1941.

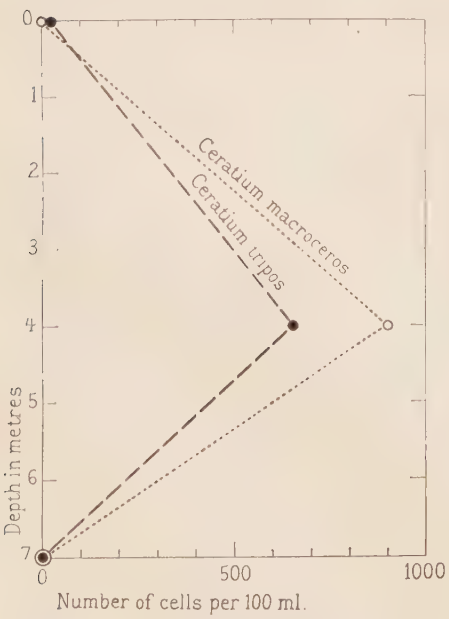


Fig. 44. Vertical distribution of *Ceratia* 1.8.1940.

Ceratium tripos (O. F. Müll.) Nitzsch.

The *Ceratia*, which generally play a significant part quantitatively in the Danish waters with the exception of the Baltic, are without any quantitative importance in the Isefjord. According to Ostenfeld 1913 this is also the case as regards the Limfjord. *Ceratium tripos* was found in the Isefjord from June to December. With the exception of the beginning of August 1940, when 650 per 100 ccm. were found in the Outer Broad at a depth of 4 m., it was always very few specimens that were observed. At the station in the Outer Broad considerable amounts of this and other *Ceratium* species were found on August 1st, 1940. The vertical distribution was interesting. In the surface layer there were in all 20 *Ceratia* per 100 ccm., at a depth of 4 m. 2,100 per 100 ccm., and at a depth of 7 m. 0. The large *Ceratia* have a quite considerable power of locomotion and under calm conditions will move to the depth with the best conditions of light. Fig. 44 shows the vertical distribution of *Ceratium tripos* and *Ceratium macroceros* in the Outer Broad on August 1st, 1940.

Ceratium macroceros (Ehrbg.) Cleve.

This species has only been observed in the Isefjord on August 1st, 1940, viz. in the Outer Broad at a depth of 4 m. (900 per 100 ccm.).

Ceratium longipes (Bail.) Gran.

Behaves completely like the preceding species. 250 per 100 ccm. were found in the Outer Broad at a depth of 4 m. on August 1st, 1940.

Ceratium bucephalum Cleve.

This species also behaves like *C. macroceros.*

Ceratium lineatum (Ehrbg.) Cleve.

A single specimen was observed in the Inner Broad in August 1940. The species was found at the same time in the entrance area.

Ceratium fusus (Ehrbg.) Dnp.

A few specimens were found in the Outer and the Inner Broad in June and August 1940.

D. Cyanophyceae.

Anabaena baltica Johs. Schmidt.

Small amounts of this species were found in June 1940 in the whole of the fjord and in August 1942 in the Inner Broad.

Aphanizomenon flos aquæ (L.) Ralfs.

A few specimens were observed in August 1940 (the Outer Broad) and October 1940 (the Inner Broad).

Microcystis sp.

A species with an average size of cell of 2.5—3 μ was found in the whole of the fjord from June to October 1940, furthermore in August 1942 and July 1943. Only in August 1940 the number of colonies was of any significance, viz. about 2,000 per 100 ccm.

Coelosphaerium sp. sp.

In the beginning of August 1940, in all parts of the fjord, but particularly in the Inner Broad, considerable amounts (about 50,000 colonies per 100 ccm.) were found of two species belonging to this genus. The species forming the largest colonies is presumably *C. naegelianum* Unger.

Otherwise this genus was not observed.

Chroococcus limneticus Lemm.

In June—August 1940 and August 1942 this species was found in the Isefjord in quantities up to 3,000 colonies per 100 ccm.

Undetermined Chroococcaceae.

Rather considerable amounts of Chroococcaceae which could not be determined, were found in June—October 1940, in August—September 1942 and in May—July 1943.

E. Flagellates.

Because of the poor preservation it is only possible to give a very incomplete list of species of flagellates. The numerically most important species generally are not specified. They may even have disappeared completely during the preservation. In return various unicellular green algae have been included in the group of flagellates, thus amongst others a *Carteria* species which in summer was sometimes present in a number of several thousands per 100 ccm.

Dinobryon pellucidum Levand.

This species, which is easily recognized, was found in a number of 3,000 cells per 100 ccm. in the Outer Broad in June 1940. Otherwise the species has not been observed in the fjord.

Pontosphaera Huxlei Lohm.

In summer this coccolithophorid belongs to the dominant species in the Kattegat (see Steemann Nielsen, 1940). In the Isefjord it is without any material importance. In 1940 it was found in the entrance area of the Isefjord (August and October). In the Inner Broad it was found in June 1942 (2,000 per 100 ccm.). Single specimens of various other coccolithophorids have also been found: *Pontospheara Bigelowi* Braarud (July 21st, 1942), *Syracosphaera* sp. (Outer Broad August 1st, 1940), and *Acanthoica* sp. (June 16th, 1942).

Distephanus speculum.

A few specimens were found in August—November 1940 and 1941.

Ebria tripartita.

Small amounts of the species were found in August—October.

Chapter Five

THE BENTHOS VEGETATION

A. Survey of the Investigations.

While the distribution of the great majority of benthos plants in the Danish waters are very well known, descriptions proper of the vegetation in the various localities, apart from the soft bottom, are rare. In Kolderup Rosenvinge's large works on algae, continued by Lund (1909—1950) there are no descriptions proper of the vegetation, even though much information about the vegetation may be derived from these works. (A survey of the distribution of the red algae in Danish waters is found in Kolderup Rosenvinge, 1935). Conditions are much more favourable with regard to the vegetation on the soft bottom, on which particularly Ostenfeld, 1908 and 1918, and Iversen, 1934, have given important contributions. Ostenfeld in 1918 gave an excellent description of the Randers Fjord, which in some respects resembles the Isefjord. From one area of the Isefjord there is also an excellent brief description by Kolderup Rosenvinge in a paper by Petersen, 1891, and Kolderup Rosenvinge has collected material in other parts of the Isefjord area though without on this basis giving any description of the vegetation. The journals from these investigations have been at my disposal. Lund, 1934, gives a thorough description of the flora of Stege Nor, Möen.

The collections for the present investigations were made in 1941—1944. I partly at various times made excursions by the motor boats of the Ministry of Fisheries and of the Biological Station and partly made collections from shallow water during bicycle rides along the shores of the fjord. In Tables 20—59, p. 85—p. 109 there is a survey of the benthos vege-

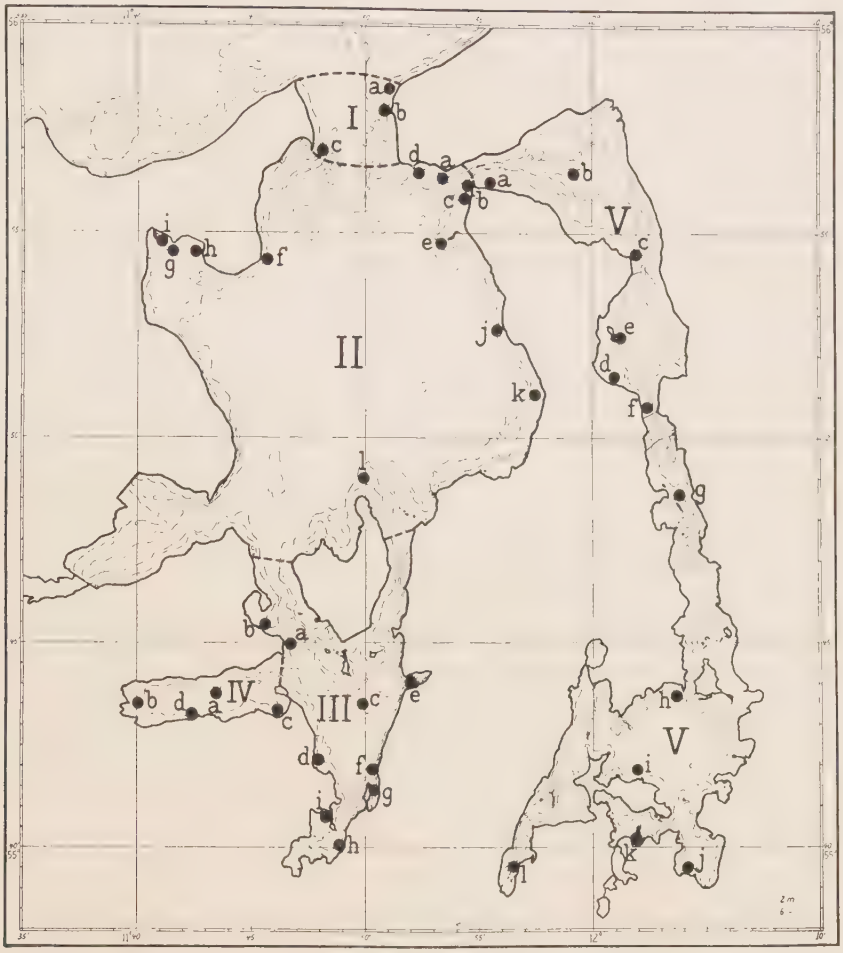


Fig. 45. Areas and stations for the benthos vegetation.

tation in the various localities. Finally, Chapter 6 is a survey of the distribution of the species in the Isefjord area.

The following section should by no means be considered a monograph of the benthos vegetation of the Isefjord; they should rather be considered a survey. The lists of plants are far from being complete, as a definitive determination of several difficult genera has been excluded beforehand. Such determinations should only be made by real specialists. While a number of more or less rare, inconspicuous species have no doubt been overlooked during the investigations (inconspicuous epiphytes have not been especially investigated), the dominant species have of course all been included, although exceptionally here, too, not all determinations have been carried out definitively, e. g. as regards the difficult genus of *Enteromorpha*. My primary endeavours have been to show the broad outlines of the distribution of the vegetation

in the fjord in connexion with an elucidation of the ecological factors which must be supposed to be of importance.

Unfortunately it was not possible to make actual quantitative determinations of the benthos vegetation, neither as regards the population nor the annual increase. By estimation it has been tried to take a fair survey of the size of the population, which may of course at most be of a relative character. At greater depths, where the algae are only seen when coming up in the dredge, it is impossible to make an only fairly correct estimate of the amount of algae. At quantitative investigations at a considerable depth the best thing would presumably be to employ a diver at the collection, as was done with great profit by Gislén, 1930.

I am much obliged to Mr. S. Lund, M. Sc., who has determined some species which were critical to me. Information about the vegetation on the southern pier of Hundested harbour is chiefly due to him.

Outside the fjord no material was collected; so the information available in the late Professor Kolderup Rosenvinge's journals has been used for comparison.

The Isefjord area has been divided into five subareas: I: the entrance area, II: the Outer Broad, III: the Inner Broad, IV: the Holbæk Fjord, V: the Roskilde Fjord; see the chart, fig. 45, where all localities of the collections have been indicated, each with a station number. Although the subareas must be considered quite naturally defined, the boundaries between some of them are somewhat vague, e. g. the boundary between II and III. It would have been easy to divide the area into a much greater number of subareas, thus it would be natural to characterize the Lammefjord as a special subarea. The reason why this has not been done is that no investigations were made there. The fact that Subarea V, the Roskilde Fjord has not been subdivided into various subareas is due to the gradual change of vegetation from the mouth of the fjord to its head, which only with difficulty allows of setting up definite boundaries.

In a previous work in Danish (Steemann Nielsen, 1944) I have proposed the introduction of new names of the various vertical zones of the sea bottom. The reason for this was the great confusion prevailing as regards the use of the terms generally used: supralittoral zone, littoral zone, sublittoral zone, etc., as different investigators may interpret the same term in quite different ways.

In the system described below, in which purely physical factors condition the division, it has been attempted in the names themselves to create concepts which cannot be misunderstood and which explain the division. The names of the main areas, the phytal and the aphytal region, are not, however, chosen quite consistently as these terms have been transferred from other systems (e. g. Remane, 1940). As they have always been used unambiguously, and as one does not like to coin more new words than strictly necessary, they have been retained.

The height of the water is used as basis of the division of the phytal region. (The aphytal region is not divided here, as only autotrophic plants are considered).

I. The Phytal Region: the area in which conditions of light allow the presence of autotrophic plants.
   (1) Adythal[1] zone. Is regularly reached only by the spray of the waves.
   (2) Hemidythal zone. Alternately above and below the water.
   (3) Eudythal zone. Always below water.

II. The Aphytal Region: the area in which conditions of light do not allow the presence of autotrophic plants.

[1] Coined from the passive form of Greek *dúō* 'I submerge'.

The boundaries between the various zones in the phytal region are difficult to define. The boundary between the eudythal and the hemidythal zone is fairly easily defined, as it is identified with the lowest water of the year. It is more difficult to define the boundary between the adythal and the hemidythal zone. As shown by a number of investigators (see Du Rietz, 1947) other rules of the distribution of plants apply to an exposed coast than to a protected coast. Du Rietz formulated this as follows: "Der Hochwasserlinie der geschützten Ufer entspricht biologisch auf dem exponierten Ufer nicht die dortige Hochwasserlinie, sondern die obere Grenze der Sturmwellen." And he further states: "Eine hydrographische Definition unserer Vegetationsgrenze erscheint tatsächlich unerreichbar." "Nur durch die Lebewelt selbst lässt sich unsere Grenze . . . einwandfrei definieren." I quite agree with the former statement, but not with the latter. The numerous attempts at characterizing the limit by means of plants have without exception miscarried, as just shown by Du Rietz. The limit at the Norwegian west coast is now according to Levring 1937 put at the uppermost limit of the *Balanus balanoides* association.

Considering the extreme difficulties of fixing a boundary between the adythal and the hemidythal zone in such a way that it considers the special conditions in the most varied localities, I have returned to the more old-fashioned way of defining the two zones. I put the mean high-water level as the boundary. In many—presumably most—localities this line is without any importance at all for the distribution of the plants. This applies especially to exposed localities. In a description of a locality we thus have this locality characterized amongst other things by stating what plants enter the adythal zone and how high into it they will go.

The mean water level in the Isefjord was established by means of the tide poles found in the harbours and at the naval station in the Inner Broad.

The upper limit of the eudythal zone in the Isefjord complex is at — 1 m., as a low water of this magnitude is common in the fjord and can be maintained for days. The upper zone of the hemidythal zone is put at + 10 cm., as the zone is generally washed to this height every day.

The following sections are a brief survey of the composition of the benthos vegetation in the fjord. Reference is made to the more detailed information to be read out of the lists of plants in the tables of Ch. VII. There will be no sociological description proper of the vegetation.

B. The Entrance.

The limit towards the Kattegat is put at a curve from Korshage to Spodsbjerg, while the southern limit is put at a curve from Skansehage to the southwestern corner of Hals Næs.

As to the algal vegetation of the adythal and hemidythal zones this area is hardly distinct from the north coast of Zealand towards the open Kattegat in places with the same conditions of the bottom. Salinity and temperature are also more or less the same. The average temperature in the surface layer of the warmest month, July, in the entrance to the fjord is 17.5° C. (1895—1916), while in the same month it is 16.5° C. at Schultz Grund lightship in the southern Kattegat. Such a difference is presumably of no importance to surface species, the more so as also the summer temperature in the Kattegat will be somewhat higher nearer the coast than at Schultz Grund lightship. As to the effect of the surf the entrance area of the Isefjord is on the whole nearly as exposed as the Kattegat coast.

The specific flora of the lower part of the eudythal zone in the Kattegat to a very small extent enters the entrance area of the Isefjord. This is primarily due to the relatively low depths there; but also the fact that the water-masses often are not stratified and thus effect that high

temperatures can be found from surface to bottom in summer, some deep-sea species thus being excluded even though conditions of light perhaps might otherwise have permitted their presence. The salinity, which on an average is not much higher than in the surface layer (19.4 ‰) is no doubt influential as well. For comparison it may be mentioned that the annual mean salinity at a depth of 15 m. at Schultz Grund lightship in the southern Kattegat is 25.9 ‰.

Among specific species from the lower part of the eudythal zone in the Kattegat occurring in considerable amounts in the entrance area of the Isefjord may be mentioned: *Delesseria sanguinea*, which, however, already in July because of the high temperature has dropped its leaves. Further there are small amounts of *Membranoptera alata* and *Brongniartella byssoides*. A single specimen of *Laminaria digitata* was found in the northernmost part at a depth of 8 m. on the bivalve Modiola. Otherwise no *Laminaria* was found in the Isefjord.

Only on the piers at Hundested any considerable vegetation has developed in the adythal zone. On the large stones on the southern pier, up to a height of 1 m., there are carpets of the blue-green alga *Calothrix scopulorum*, with various other blue-green algae and diatoms intermixed. On the northern pier *Calothrix* reaches a little higher (at any rate to + 1.3 m.). In the lower part of the adythal zone there are (from + 0.13 m.) small patches of the red alga *Porphyra leucosticta*. *Calothrix* goes down into the hemidythal zone.

On the coast north of Hundested harbour the vegetation of *Calothrix* and similar species is very insignificant, even where there are big stones in the adythal zone. This is presumably due to grinding of sand, which at an on-shore gale no doubt can be very considerable there. The piers, which stand in somewhat deeper water, are not exposed to the effect of the transportation of sand to the same degree, at any rate not in the upper zones.

In the upper part of the hemidythal zone, the upper limit of which is put at + 0.10 m., a rich vegetation is also generally found on the Hundested pier only. According to Hagerup, 1944, *Gloiosiphonia capillaris* and *Polysiphonia Brodiaei*, amongst others, are found on scattered stones in shallow water on Lynæs Sand. As the 2 m. curve is not found until about 1,000 m. from the beach and Hundested harbour protects the place, the surf is not particularly violent there. Thus there is a possibility of an algal vegetation more or less corresponding to conditions near the beach west of Kulhus harbour (see p. 91).

Table 21 gives a description of the vegetation on the outer side of the southern pier in Hundested harbour. A great many vertical zones are found. While *Enteromorpha* sp. is found among the dominant species from + 0.08 m. to — 0.07 m., *Ceramium diaphanum* has its upper limit at the mean water level and is found among the leading species down to — 50 cm. At the upper limit it was clearly faded. *Polysiphonia nigrescens* has its upper limit at — 0.07 m., while *Fucus vesiculosus* and *Fucus serratus* have their upper limit at — 0.30 m., and below 0.50 m. are the completely dominant plants down to about 2 m. On the sea floor below this depth *F. vesiculosus* decreases greatly, and *F. serratus* and *Furcellaria fastigiata* are the absolutely dominant species. From about — 6 m. also the red alga *Delesseria sanguinea* generally belongs to the dominant plants.

Halidrys siliquosa, which, as will be shown below, belongs to the dominant species in the Outer Broad, was found only once at a depth of 5 m. off Spodsbjerg lighthouse.

Beside the stones the bottom exclusively consists of sand in the entrance area. Previously there have been great populations of *Zostera marina*, e. g. on Lynæs Sand. After the appearance of the epidemic disease of the grass-wrack about 1933 this plant practically completely disappeared from the whole area and as late as 1943 had returned only to a very small extent. Thus the whole of Lynæs Sand was crossed under conditions of the weather in which the bottom

was clearly visible without one plant being observed. But on the western side of the entrance a sporadic population of *Zostera marina* was observed. A single plant was also observed at a depth of 9 m. in the eastern area near the boundary towards the Kattegat. It is presumably the considerable current in the entrance area in connexion with the frequent surf which prevents a re-establishment of *Zostera marina* as this plant in the years 1941—1943 was again forming large populations farther into the fjord.

C. The Outer Broad.

The benthos vegetation in the Outer Broad greatly resembles that of the entrance area. Still, there are many characteristic differences. Thus none of those species of the Kattegat which are specific of the lower eudythal zone penetrate into this area. Not even *Delesseria sanguinea*, which at a certain depth was among the dominant plants in the entrance area, does so. Various species from the hemidythal zone are also found in the entrance area only. Thus e. g. *Bryopsis plumosa*, which is common on the pier at Hundested at a depth of about 0.5 m., has not been found farther into the fjord. *Petalonia fascia*, which on the southern mole at Hundested at any rate for some years was found in a fringe in the upper part of the hemidythal zone, behaves in a similar way.

In return there are in the Outer Broad a few species which are missing at the open Kattegat coast and in the entrance area because of the more unsettled conditions. Such a typical species is *Fucus spiralis*. It is not found along Zealand's open coast of the Kattegat, nor in the entrance area of the Isefjord, e. g. on the piers at Hundested.

In the Outer Broad it has been found in various places sheltered from a strong surf and with clean water. These places are the inside of the breakwater at Lynæs harbour and the outside of the eastern pier in the same place. According to Professor Kolderup Rosenvinge's journals it is, moreover, found on the northern outer end of a breakwater immediately north of Rørvig harbour. According to kind information from Dr. T. W. Böcher it is still found there.

Various species which in the entrance area are not found until a depth of at least 5 m, and there only in a small number of individuals, are found in the Outer Broad from much lower depths and in a considerable amount. Thus *Halidrys siliquosa* was found only once in the entrance area, at a depth of 5 m., whereas in the Outer Broad it belongs to the dominant species at depths of 2—4 m. *Chorda filum* in the entrance area behaves quite like *Halidrys*. While considerable amounts are generally found in the Outer Broad at depths from about 1 to 5 m. and may also be observed in shallower (and also deeper) water, few specimens have been found in the entrance area, at depths of 5—8 m. It is undoubtedly the unsettled conditions which effect that these species cannot be found in shallower water in the entrance area.

As to the vegetation on a soft bottom the difference between the entrance area and the Outer Broad is still more pronounced. Movements of the water assert themselves much more on a soft bottom. Whereas hardly anything grows on the sandy bottom in the entrance area—only a few sporadic specimens of *Zostera marina* at rather great depths—conditions are quite different in the Outer Broad.

In fairly well protected places—particularly where the bottom slopes slowly outwards—large populations of *Ruppia* are found from about — 15 cm. It is presumably especially *Ruppia spiralis*, of which great amounts are found in a fertile state. The very low populations, however, as a rule presumably are *R. maritima*, but these plants generally are sterile. *Zostera Hornemanniana* occurs sporadically from — 20 cm. *Zostera nana* is found in the same area (at most

reaching — 5 cm.). *Zostera marina* occurs from about — 0.6 m. *Zannichellia palustris* is found here and there at depths of a few metres, and *Potamogeton pectinatus* was found by Kolderup Rosenvinge in low water south of Rørvig. *Ruppia* and *Zostera nana* are absent in exposed places (particularly where the shelf slopes more steeply). In a few places *Zostera Hornemanniana* was not found either.

In the Outer Broad *Zostera marina* at the time when the investigations were made there (1941 and 1942) had not reached its former density (information from people familiar with the locality), even though it had returned in most places. It only went down to a depth of about 4 m.

Zostera marina has never covered the bottom of the basin proper in the Outer Broad. Here the depth is about 9—10 m. (see the chart in Petersen, 1891). Even if the light, as appears from Chaper One, F, p. 21, is intense enough for an autotrophic vegetation down there, there is no possibility for *Zostera marina* to live there, since it is a light species, as e. g. appears from its normal vertical distribution in the Kattegat (see Ostenfeld, 1908). Still, it must be supposed to have gone farther down in the Outer Broad than was the case in 1941—1942. Conditions in the Roskilde Fjord, where exact information from the time before the disease of the grass-wrack is available, in connexion with the present investigations clearly show that the grass-wrack at its return first appeared in rather shallow water. It seems natural that a re-immigration should start in the vertical zone with optimum conditions. This is perhaps the more probable as *Zostera marina* is a perennial. In the extreme localities, in the present case at the greater depths, the grass-wrack can presumably only start under particularly favourable conditions; but if the species has got started it will be able vegetatively to form greater populations.

As mentioned on p. 5, there are stones nearly everywhere in shallow water in the Outer Broad. These are generally scattered more or less, but stone reefs proper have formed in a few places. We shall now take a survey of the vegetation on these stones, with further reference to the tables on p. 89 ff. The adythal zone is clearly developed only on piers and in similar places.

The hemidythal zone, ranging from the mean high water level (about + 0.10 m.) to a little less than — 1 m., generally displays an at any rate quantitatively rich vegetation, which, however, does not begin until about — 0.15 m. *Fucus vesiculosus* is the dominant species. Furthermore there are generally considerable amounts of *Ralfsia verrucosa* and *Rivularia atra*. A very large amount of *Nemalion multifidum* is found in summer, and in the spring months *Scytosiphon lomentaria*, which occurs right up to the mean water level. Furthermore *Monostroma Grevillei* is found at this time. Where freshwater oozes out there are generally great quantities of *Enteromorpha*. On *Fucus vesiculosus* there are generally some epiphytes, among which special mention should be made of *Stilophora rhizoides* and *Ceramium diaphanum*. Most of the species found on *Fucus* in the eudythal zone are also found in the hemidythal zone.

The upper limit of the eudythal zone fairly coincides with the upper limit of *Fucus serratus*, of which at any rate only scattered specimens are found in the very lowest part of the hemidythal zone.

Fucus vesiculosus and *Fucus serratus* are dominant at depths of 1—2 m. Only scattered specimens of *F. vesiculosus* are found below 2 (at most 3) m. Down to about 3 m. *Fucus serratus* and *Halidrys siliquosa* are the dominant species. On Alholm reef, where the latter species does not play any considerable part, *Furcellaria fastigiata* and *Fucus serratus* were dominant at this depth.

The upper limit of *Halidrys* in the Outer Broad is at about — 1.5 m. On Næsby reef it

already belongs to the dominant plants at this depth. Considerable amounts of it are found down to a depth of 4 m. Below that depth it is practically absent, as it was observed only once at a depth of 6 m. *Fucus serratus*, which below 3 m. is only found sporadically, has been observed down to depths of 8—9 m., i. e. so far down as stones have been found at all in the Outer Broad.

From about — 5 m. *Furcellaria fastigiata* is the dominant species. *Ceramium rubrum* and *Polysiphonia nigrescens* may sometimes also belong to the dominant plants at these depths.

Besides the dominant plants there are at the various depths a great number of other species, several of which are often present in no small quantities (see Tables 23—34).

In the course of June large amounts of the green alga *Cladophora sericea* appear, which in a detached state twists itself round the benthos plants. At the beginning of July *Cladophora sericea* disappears, as it is carried towards the shore by wind and current.

D. The Inner Broad.

Just as the benthos vegetation of the Outer Broad is qualitatively poorer than that of the entrance area, so the Inner Broad is poorer in this respect than the Outer Broad, but quantitatively there is absolutely no decrease in the Inner Broad.

The most characteristic feature of the Inner Broad in relation to the Outer Broad is the complete absence of the large brown alga *Halidrys siliquosa*, which in the Outer Broad belongs to the dominant species at depths of 2—4 m. Among other species characteristic of the vegetation in the Outer Broad which were not found at all in the Inner Broad we may mention *Ahnfeltia plicata*, *Leathesia difformis*, *Nemalion multifidum*, *Stilophora rhizoides*, and *Chordaria flagelliformis*. Furthermore, a number of other species found here and there in the Outer Broad were not observed in the Inner Broad at all, e. g. *Fucus spiralis* and *Zannichellia palustris*. The cause of the absence of the latter plant in the Inner Broad is—as we shall see below—quite another than in the case of the other species.

It is characteristic of *Fucus vesiculosus* and *Fucus serratus* in the Outer Broad that they have large growths of epiphytes on the old parts of the thallus. This feature is rare in the Inner Broad.

The vegetation on a soft bottom is very similar to that found in similar places in the Outer Broad. In the exposed places where the bottom slopes steeply, i. e. the greater part of the east shore, where the soft bottom in shallow water consists of pure sand, there are on the whole no plants down to about — 1 m. This is the case of nearly the whole coast of Horns Herred north of Eiby. In this area small amounts of *Zostera Hornemanniana* were found where there was some protection by stones.

On the sandy bottom of Vellerup Vig there are from about — 0.30 m. small amounts of *Ruppia* with patches of *Zostera nana* and *Zostera Hornemanniana*. A similar vegetation is found on the opposite side of the broad where there is a sandy bottom, e. g. off Bognæs and in the outer parts of Udby Vig.

Only *Ruppia* is found in the places where the bottom in shallow water is very soft, e. g. in Tempelkrog off Eriksholm, but then extensive populations of it are present.

Where the coast slopes gently or is otherwise protected, *Zostera marina* is found already from about — 0.5 m. In more exposed places this plant is not found until below about — 1 m. The depths to which *Zostera marina* goes out differ somewhat. Normally it was only found down to a depth of about 3 m. It was easy to see the regeneration of *Zostera marina* during the years 1940—1943. While e. g. in 1940 there were only a few plants here and there off the

naval station, real meadows of the species were found there in the summer of 1942. According to statements made by the fishermen the *Zostera* meadows in Bramsnæsvig in 1943 were of the same extent and density as before the arrival of the disease.

The greatest depth to which *Ruppia* (*Ruppia spiralis*) was found was — 1.5 m. A single specimen of *Potamogeton pectinatus* was found in Tempelkrog off Strandskoven at a depth of — 2.5 m. This species and *Zannichellia palustris* were otherwise absent from the Inner Broad as well as from the Holbæk Fjord.

Fucus vesiculosus was found everywhere on large stones from about — 30 cm. In places where there are small stones and where the bottom otherwise is not particularly soft there is moreover a great number of other species. The composition of species varies with the seasons, some of the species being annuals. The position of the place the character of the soft bottom and the wave action—is also of great importance. In Vellerup Vig, where the bottom is sandy beside the stones and where the effect of the surf is not very great, a luxuriant growth of algae was found on small stones from about — 30 cm. in the summer months. Particularly *Hildenbrandia prototypus* and *Rivularis atra* were common, but also *Chaetomorpha aerea* and *Polysiphonia nigrescens.*

In the spring e. g. *Dumontia filiformis* and *Monostroma Grevillei,* which disappear when the heat sets in, are found in such localities.

The outside of the pier at Ejby (see Table 40), which is built of large stones, displays a special composition of plants. In the adythal zone *Calothrix scopulorum* is found in summer (from + 50 cm. to the mean water level). In the hemidythal zone we find at the top (from about — 20 cm.) *Hildenbrandia prototypus* with patches of, amongst others, *Ceramium rubrum* and *Monostroma Wittrochii. Fucus vesiculosus* is dominant from about — 35 cm.

In the upper part of the eudythal zone (from — 1 to — 3 m.) *Fucus serratus* is dominant everywhere in the Inner Broad on large stones. At the upper limit of the zone there are also great amounts of *Fucus vesiculosus.* This species generally is not found below about 2 m. (off Bognæs, however, it was found at a depth of 4 m.). Large amounts of *Furcellaria fastigiata* may also be found in the uppermost part of the eudythal zone (it also ascends to about — 30 ccm. in the hemidythal zone). Similarly *Chorda filum* abounds, which, however, is mostly attached to small stones or bivalves. Where there are no big stones, *Chorda* is absolutely dominant. *Polysiphonia nigrescens* may also be abundant in the upper part of the eudythal zone. Below about — 3 m., the lower normal limit of *Fucus serratus* in the Inner Broad, *Polysiphonia nigrescens* is generally the dominant species together with *Chorda filum* and *Furcellaria fastigiata.* A large stone which had been fished from a depth of 6 m. in the northwestern part of the Inner Broad by a diver, was overgrown with *Phyllophora Brodiaei.* In my own collections this species was scanty. On the whole the dredge is not the best implement for obtaining a proper impression of the composition of the vegetation at the somewhat greater depths.

Detached algae are found lying on the bottom in many places in the Inner Broad. However, they are of no great importance. Quantitatively very little is brought up by the dredge.

In June there are great amounts of detached *Cladophora sericea* as in the Outer Broad. All algae at depths of 1—2 m. and to a smaller degree also somewhat farther down are entangled in this green alga. In the course of July large amounts of *Cladophora sericea* are cast ashore in various places, e. g. in Udby Vig. When a gale at this time has cleaned the algal populations of the green alga, no great amounts reappear. Later in summer a similar alga, *Chaetomorpha Linum,* is dominant. During the years of investigation the amount of this alga was far from being as large as the amount of *Cladophora sericea* by the end of June.

In the places in the fjord where freshwater oozes out from the land, there is generally a vigorous fringe of *Enteromorpha* (chiefly *Enteromorpha intestinalis*) immediately around the mean water level on stones and in similar places.

E. The Holbæk Fjord.

The qualitative composition of the benthos vegetation in the Holbæk Fjord is much poorer than that in the Inner Broad. Thus there is a gradual decrease starting from the entrance area of the Isefjord and continuing in the Outer and Inner Broad to end in the Holbæk Fjord. *Fucus serratus*, the dominant species in the upper part of the eudythal zone in the Inner Broad is completely absent in the Holbæk Fjord.

One of the causes of the small number of species in the Holbæk Fjord is the lack of stones, these being found only down to a depth of about 2 m. This cannot, however, be the cause of the absence of *Fucus serratus*, as this species is dominant at depths of 1—2 m. in the Inner Broad.

It is the plants of the soft bottom which characterize the vegetation in the Holbæk Fjord.

From about — 25 cm. there are extensive populations of *Ruppia* (both *R. maritima* and *R. spiralis*); furthermore there are small amounts of *Zostera Hornemanniana*. In the summer of 1941 considerable populations of *Zostera marina* were found at depths from about 1 to 3 m. In this year it was, however, still far from having reached its previous quantitative occurrence. *Ceramium rubrum* is found as an epiphyte on *Zostera* leaves. Some algae are found detached on the bottom. During gales great amounts of these are washed ashore, chiefly the red alga *Ceramium rubrum*, but occasionally also the green alga *Enteromorpha*.

In the summer of 1941 and of 1942 large detached amounts of the green alga *Ulva lactuca* were found in the exterior part of the fjord within Kirsebærhage. It was chiefly found at a depth of about 50 cm. The individual thalli might reach a diameter of at any rate 30 cm.

Small amounts of *Fucus vesiculosus* grow on the larger stones in the hemidythal zone (from about — 40 cm.). This population is quantitatively considerably smaller than that of the Inner Broad. The plants look somewhat degenerated, although air bladders have generally developed. Near the mean water level there are generally large amounts of *Enteromorpha*, amongst others the species *E. intestinalis*. Great amounts of *Chorda filum*, *Furcellaria fastigiata*, and *Ceramium rubrum* are found on stones at depths of 1—2 m. All algae are densely covered with epiphytes, particularly diatoms. A particularly characteristic feature of the Holbæk Fjord is the growth of the infusorian *Vorticella* on the algae.

F. The Roskilde Fjord.

Just as the benthos vegetation gets qualitatively poorer as we pass from the Outer to the Inner Broad and go on to the Holbæk Fjord, so it does when we enter the Roskilde Fjord and continue into its innermost parts. Conditions are not, however, identical, as, in contrast to the Isefjord, there is in the Roskilde Fjord, as shown in Chapter One, a decrease in salinity towards the interior. While the decrease in salinity is of no material importance to the vegetation of marine algae proper, as appears from the fact that the species of the Outer Broad are found in other places in the Danish waters at similar salinities as that of the Roskilde Fjord, conditions are different as regards the various brackish water species. *Zannichellia palustris*, which is found in a few places in the Outer Broad, but was not observed at all in the Inner Broad

and the Holbæk Fjord, was found in many places in the Roskilde Fjord, right into its innermost branch, the Lejrevig, among the dominant species. *Potamogeton pectinalis* behaves in the same way. Only a single specimen of this species was observed in the Inner Broad.

As the vegetation changes from the place where the Roskilde Fjord debouches into the Outer Broad of the Isefjord at Kulhus to the inner branches of the fjord, it is not possible to give a single description. The best survey is obtained by following the change of the vegetation from station to station (see Tables 48—59).

In the outermost broad of the Roskilde Fjord, at Frederiksværk, the vegetation on stones on the whole corresponds to that of the Inner Broad. Thus *Fucus serratus* is the dominant species in the uppermost part of the eudythal zone, while *Halidrys siliquosa* was not observed. In the lower part of the eudythal zone primarily annuals were found on stones. In 1941 *Chorda filum*, which was also common in the upper part of this zone, was dominant together with *Ceramium rubrum* and *Polysiphonia nigrescens*. In June 1942 *Chorda filum* was not found at Brovig, but the two other species were. *Phyllophora Brodiaei* and *Furcellaria fastigiata* were the most abundant perennials. Large amounts of *Fucus vesiculosus* were found on the big stones in the hemidythal zone (down to a depth of 2 m.), while furthermore a number of different species were found there, especially on small stones.

On the soft bottom there are in the hemidythal zone (— 20 to — 100 cm.) populations of *Ruppia* with small amounts of *Zostera Hornemanniana* and *Zostera nana*. In the upper part of the eudythal zone (about — 1 to about — 2m.) there were (1941—1942) large meadows of *Zostera marina* with admixture of *Zannichellia palustris* and *Ruppia spiralis*.

At somewhat greater depths (3—4 m.) *Zannichellia* was dominant, and there were small amounts of *Zostera marina* and *Potamogeton pectinatus*. The abundance of *Zannichellia* at these depths was no doubt due to the fact that *Zostera marina* had not yet at that time regenerated completely. It appears from Kolderup Rosenvinge's dredgings at the beginning of the century that *Zostera* then was completely dominant there. As stated above, the large growths of *Zostera* in the Isefjord complex reappeared first in the uppermost parts of the eudythal zone after the disease of the grass-wrack was over. In 1942 the plant was observed down to a depth of 5 m. *Zannichellia* was observed down to a depth of 6 m. No benthos plants have been observed in the deep of the channels in the Roskilde Fjord.

In the bight of Frederiksværk on the coast of Halsnæs, e. g. off the farm of Grønnæsse, typical salt-marshes with sand- and clay-binding Cyanophyceae were found in the uppermost part of the hemidythal zone, *Microcoleus chtonoplastes* being the dominant species. Such a vegetation presumably also occurs in a few other places in the Roskilde Fjord. It is also found in the Outer Broad of the Isefjord within Alholm off the coast of Hornsherred.

No more *Fucus serratus* is found south of the broad of Frederiksværk. On the stones in the hemidythal zone there we find *Fucus vesiculosus*, in the eudythal zone annual red algae, particularly species of *Ceramium* and *Polysiphonia*.

In the hemidythal zone the soft bottom is covered with generally very dense populations of *Ruppia*. The eudythal zone is overgrown with *Zostera marina* down to a depth of 6 m. In 1942 there were very large and dense populations of this species about — 2 m. Furthermore *Potamogeton pectinatus* was found. In the early summer great amounts of detached *Cladophora sericea* were observed there (as everywhere in the Isefjord complex). In the late summer great amounts of detached *Chaetomorpha Linum* and *Ulva lactuca* were found in shallow water. Farther south great quantities of *Chorda filum* occurred on a bar of oyster shells (from the Littorina period). Off Horsehage, where there were no stones in the eudythal zone, there were

large meadows of *Zostera marina* and at a depth of 2 m. there were furthermore rather considerable amounts of *Potamogeton pectinatus* and *Zannichellia palustris*. Considerable amounts of *Zostera* were found even at a depth of 5 m. (1942).

Large meadows of *Zostera marina* were found in the innermost large broad (off Bognæs) at a depth of 2 m., while at a depth of 4 m. there were shell deposits without any vegetation.

Fucus vesiculosus (generally without air bladders) and *Ralfsia verrucosa* were found on stones in the hemidythal zone in the very innermost branch of the Roskilde Fjord (Lejrevigen). Large growths of *Ruppia* (both *R. maritima* and *R. spiralis*) with an admixture of *Zannichellia palustris* were found on the soft bottom from about — 25 cm. to about — 40 cm. *Potamogeton pectinatus* grew immediately outside this area and *Zostera marina* from about — 60 cm.

G. The Factors Effecting the Distribution of the Benthos Species in the Isefjord Complex.

In the preceding sections we have seen how the vegetation changes from one area to the other in the Isefjord complex. We shall now try to elucidate the causes of these changes, discussing apart various factors which may be supposed to be of importance to the distribution.

(a) *Salinity.*

While the mean salinity of the surface layer in the entrance area is of the same order of magnitude as that of the southern Kattegat (mean salinity at Rørvig 19.4 ‰, at Schultz Grund lightship 18.6 ‰), conditions are quite different in the deep. At Schultz Grund lightship the mean salinity at the bottom (a depth of 26 m.) is 30.6 ‰, while at the bottom in the entrance area of the Isefjord it is not very different from that of the surface layer. The highest salinity I have measured at the bottom in the entrance area was 24.1 ‰. Very often the salinity is practically the same from surface to bottom.

The fact that a great number of species from the lower eudythal zone do not enter the entrance area of the Isefjord therefore may very well be due to conditions of salinity, even though another factor—the temperature—presumably is the decisive one in this respect.

Conditions of salinity cannot be of any material importance for the distribution of the plants within the Isefjord (with the exception of the Roskilde Fjord), since, as shown above, the salinity is practically the same in the whole area. At any rate it will not explain the decrease in the number of species as we pass towards the head of the fjord.

As the decrease in the number of marine species inwards in the Roskilde Fjord runs parallel with the decrease in the Isefjord proper, there is no reason, either, to deal with the question here, the more so as the species found in the Outer Broad, with the exception of a few—first of all the brown alga *Striaria attenuata*—are found elsewhere in the Danish waters at salinities as low as that of the innermost part of the Roskilde Fjord.

Conditions are different in the case of two species among the phanerogams, *Zannichellia* and *Potamogeton pectinatus*, which have their upper limit of salinity at about 18—20 ‰ S. These species are found among the dominant species in the Roskilde Fjord (mean salinity at Frederikssund 15.2 ‰ S.), while their occurrence in the Isefjord proper (mean salinity 19—20 ‰ S.) is very sporadic. Thus *Zannichellia* was not found at all in the Inner Broad and in the Holbæk Fjord, where, if the salinity had been a little lower, one would absolutely have expected to find it. In the Outer Broad, where the mean salinity indeed at most is insignificantly lower than in the Inner Broad (see p. 11), the salinity is not so constant as in the

Inner Broad. Therefore there will be periods when this species may get an opportunity of settling. Furthermore, seeds from the Roskilde Fjord will easily be carried to the Outer Broad, but with difficulty to the Inner Broad. As to the salinity requirements of *Zannichellia palustris* and *Potamogeton pectinatus* the Isefjord is an interesting area, where their presence or absence will probably vary somewhat. Thus *Potamogeton pectinatus* was not observed in the Outer Broad at the present investigations, while the species had previously been found there by Kolderup Rosenvinge.

(b) *Temperature.*

In summer the temperature at all depths in the Isefjord complex rises to more than 20° C. (see p. 11). The mean temperature in the surface layer at Frederikssund is 18.3° C. for July, which may be considered more or less representative of all water-masses in the Isefjord complex. In the southern Kattegat (at Schultz Grund lightship) the mean temperature for July at a depth of 15 m. is 11.5° C., at a depth of 20 m. 8.2° C., and at 26 m. 7.5° C. It is true that the temperature rises somewhat there later in the year. The highest monthly temperature at a depth of 15 m. is 14.1° C. (August), at a depth of 20 m. 12.7° C. (September), and at 26 m. 12.1° C. (September).

All species which will not stand a summer temperature of the order of magnitude of 20° C., therefore have no possibility of growing in the Isefjord. This is first and foremost the case of a considerable number of the species from the deeper part of the Kattegat. As an example we may mention the red alga *Dilsea edulis,* which is common in the lower eudythal zone immediately outside the Isefjord, but which will not even penetrate into the entrance area of the fjord.

Various species which in the Danish waters (e. g. the Kattegat) are also found in the upper part of the eudythal zone, do not enter the Isefjord, either. At most a few specimens may be found in the entrance area. Among such species we may mention *Laminaria digitata,* which was found at a depth of 8 m. in the outermost part of the entrance area. The slightly higher temperatures near the surface in the Isefjord in proportion to those of e. g. the Kattegat are presumably sufficient to exclude these species, which, indeed, are of a boreal type of distribution. Even in the surface layer the mean temperature of the warmest month (July) is 2° C. higher in the Isefjord than in the southern Kattegat (Schultz Grund lightship).

Delesseria sanguinea was found in the entrance area, but was not otherwise observed in the Isefjord. At the end of July 1943 it had, however, lost the leafy parts of the thallus, while the plant at the same time still possessed these in the southern Kattegat. The vegetative period of this species thus is short in the entrance, which is no doubt due to the high summer temperature.

In winter the temperature is lower in the Isefjord than in the deep in the Kattegat. At a depth of 20 m. the lowest monthly mean (February) at Schultz Grund lightship is 3.7° C., whereas temperatures about freezing-point are found right down to the bottom in the Isefjord in the coldest months.

The fact that such a species as *Brongniartella byssoides* is not found in the Outer Broad is perhaps due to the low winter temperature.

(c) *Pollution and the Like.*

No investigations of pollution have been made in the Isefjord. As to the Outer Broad it may be stated that pollution is very insignificant.

On the inside of the condenser tubes in cooling water circuits, e. g. at power stations, a layer of slime formed by bacteria will settle if the cooling water is only just a little polluted. In the condenser tubes at the large power station at Kyndby, which takes its cooling water from the Outer Broad, such slime has never appeared. It has not yet been necessary to clean the tubes of slime. It may be stated that at one Danish power station it is necessary to clean the tubes once a week.

The sewage of the town of Nykøbing flows into the bight of Nykøbing. There are no purification works there. The pollution from there is presumably of local importance to the Nykøbing bight only.

There are no greater built-up areas around the Inner Broad. There is therefore no actual pollution from the land. A very considerable production of vegetable matter takes place in the Inner Broad. A kind of pollution probably takes place by the decomposition of this matter. For instance it is seen that there are considerable admixtures of organic particles in the bottom deposit, even in many places in shallow water. In stormy weather this matter is raised into the water together with clay particles so that it becomes quite turbid. This is of course of importance for the submarine conditions of light as was shown in Chapter One, F, p. 21. As, however, the depths in the Inner Broad are small, this cannot, presumably, be considered very important. The direct influence of the fact that the particles, when the unsettled weather conditions have ceased, will settle on the attached plants is no doubt much more decisive. Thus it is seen that in the places in the Inner Broad where the bottom slopes steeply (the coast of Hornsherred) and where the bottom outside the stones is sandy, there are commonly on stones in the hemidythal zone various species, e. g. *Hildenbrandia prototypus*, which are not found at all in the places where the shallow extends far out and the bottom beside the stones is very soft.

The content of dissolved organic substances presumably is also relatively great in the Inner Broad. The considerable intensity of respiration in proportion to the intensity of photosynthesis, as shown by the experiments on production (see Chapter Two, p. 37), indicates the presence of a considerable amount of bacteria in the water, and therefore of dissolved organic substances, too.

In the Holbæk Fjord the admixture of organic matter in the bottom deposit is still more pronounced than in the Inner Broad. In bad weather there will be an admixture of bottom material to the water-masses all over the fjord, as the depths are low everywhere. Furthermore there is an admixture of sewage from Holbæk (population: 14,000). The great amount of the infusorian *Vorticella*, e. g., which is found on the algae, suggests a direct pollution.

In winter when the fjord is frozen over, the pollution will be of particular importance, as in this case there will be a loss of oxygen, which because of the ice cannot be counteracted by exchange with the atmosphere.

In the Inner Broad the loss of oxygen is not very great (see p. 18). Still, there is a great probability that a minor reduction of the amount of oxygen can be of importance to many algae. I am inclined to interpret such a reduction as at any rate a contributing cause of the absence of *Halidrys siliquosa* in the Inner Broad. Near drains, as at Holbæk and Nykøbing, matters are different. There we must count on a complete exhaustion of oxygen. Therefore it seems natural that near drains we find only annuals in summer, as the perennials will perish in winter because of the lack of oxygen.

Such a typical annual species which may be found near drains is the brown alga *Chorda filum*. Only 25 m. from the outlet of the main sewer of the town of Nykøbing this species is abundant. Species of *Enteromorpha* also thrive where sewage is drained off.

Pollution in the widest sense of the word must be assumed to be the factor which mainly determines the distribution of algae in the whole Isefjord complex. *Chorda filum* thus is a species which will thrive practically everywhere where a suitable substratum is available. *Fucus vesiculosus* is of the same type as it is only absent in a somewhat larger area around the drains. *Fucus serratus* is more sensitive to the pollution complex and therefore is absent both in the Holbæk

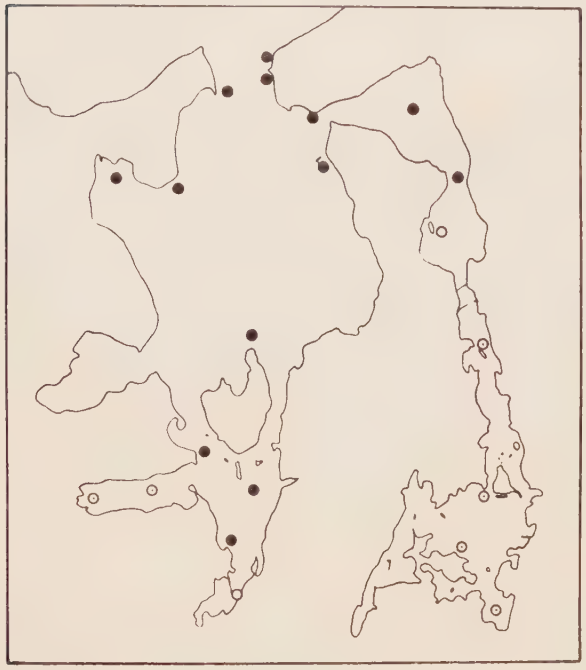


Fig. 46. Distribution of *Fucus serratus* (● present, ○ not present).

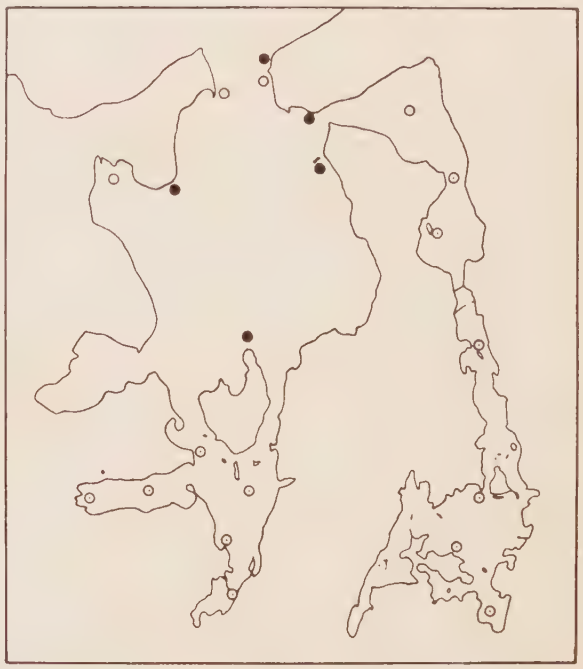


Fig. 47. Distribution of *Halidrys siliquosa* (● present, ○ not present).

Fjord and the greater part of the Roskilde Fjord (fig. 46). A still more sensitive species is *Halidrys siliquosa*, which is found only in the Outer Broad (fig. 47). *Fucus spiralis*, like *Halidrys*, is found only in the Outer Broad, even in the outermost part only.

In part it is no doubt a question of an either—or whether a species will thrive in an area or not. Thus one might have expected that *Fucus serratus* would have shown a decrease in the Inner Broad in proportion to the Outer Broad; but this is not so at all. Similarly large amounts of *Halidrys* are found at the innermost station in the Outer Broad (Næsby reef), while it was not observed at all at the outermost station in the Inner Broad (off Bognæs).

The question of pollution (in a wide sense) does not seem to be of much importance to the phanerogams, if we leave out of account conditions in the immediate proximity of the outlets of the drains. It should, however, be noted that *Zostera nana* seems to avoid a bottom with a great admixture of organic matter. This species has not been found in the Holbæk Fjord.

(d) *Conditions of Light.*

Everywhere on stones in the Isefjord complex there are attached algae, i. e. in the Outer Broad down to a depth of about 8 m. and in the Inner Broad down to about 6 m. On the soft bottom at greater depths there is no attached vegetation. In the whole of the Outer Broad we

may, however, find diatoms and some blue-green algae, particularly an *Oscillatoria* species. *Zostera marina* was not found at the greater depths before the grass-wrack disease, either, as this species is rather euphotic.

There are no oligophotic species proper in the Isefjord, unless we consider *Striaria attenuata* as being so. In the Kattegat it is known as an exclusive oligophotic species. The species is found in the lower part of the eudythal zone in the Outer Broad. In the Inner Broad off Bognæs it was observed at a depth of $2^1/_2$ m.

The nearly complete absence of oligophotic species proper in the Isefjord is not due to conditions of light, as these at depths of 6—8 m. approximately correspond to those at a depth of about 20 m. in the southern Kattegat (see p. 27), where the typical deep-sea flora is just found. As stated above, these species require a considerably lower summer temperature than that found in the Isefjord.

(e) *The Surf.*

On the outside of the piers at Hundested there are two species of algae which are characteristic of localities with a strong surf and which have not otherwise been observed in the Isefjord area. They are *Petalonia Fascia* and *Porphyra leucosticta*. The cause of the absence of these species on piers farther into the fjord presumably is not that they absolutely require such a strong surf, but that in places with a less strong surf they are ousted by competing species.

On the piers at Hundested exposed to a strong surf, the adythal zone reaches higher than elsewhere in the Isefjord. On the pier at Ejby (the Inner Broad) *Calothrix scopulorum* only reaches up to + 50 cm., while on the south pier at Hundested it reaches up to + 1 m.

In return the strong surf in the entrance area effects that such a species as *Halidrys siliquosa*, which is among the dominant plants in the upper part of the eudythal area in the Outer Broad, is not found until farther down (5 m.).

(f) *Drying up during Low Water.*

In the Isefjord with the exception of the entrance area *Fucus serratus* was not found until at a depth of at any rate 1 m. Thus it is not found at all in the hemidythal zone, while this species elsewhere in the world, e. g. at Heligoland, is just the dominant species in the lower part of the hemidythal zone.

At Heligoland it is, however, the tide that conditions the hemidythal zone. The lower part of this zone therefore will never be exposed for any prolonged period. Conditions are different in the Isefjord. As stated on p. 12 the tidal range is small. A considerable low-water therefore will be conditioned by the wind, primarily gales from the southeast. A low-water of 1 m. may, as stated on p. 12, in the Isefjord hold out for days, *Fucus serratus*, if found above — 1 m., thus being exposed to a drying-up of long duration which would be disastrous to this species.

On the south pier at Hundested *Fucus serratus* was found already at a depth of 50 cm. Even if in this place there is a lowwater of — 1 m. for several days, there will always during such a period, also with an off-shore wind, be a swell, which conditions a surf against the pier, and *Fucus serratus* will not be exposed to any real drying-up.

Chapter Six

SURVEY OF BENTHOS SPECIES IN THE ISEFJORD AREA

Only those species are included which were observed during the present investigations (1941—1943). Therefore the list is incomplete, the more so as the determination of species has not been carried through in all cases.

Rhodophyceae.

Ahnfeltia plicata (Huds.). Common in the entrance area and the Outer Broad, particularly at depths of 1—5 m.

Brongniartella byssoides G. et W. Found in the eudythal zone in the entrance area.

Callithamnion corymbosum (Engl. Bot.) Lyngb. Present about the mean level of the sea on the pier at Hundested. Small amounts of specimens belonging to the genus *Callithamnion* were observed from the entrance area to the Inner Broad.

Ceramium diaphanum Harv. et J. Agardh. Present in the entrance area and the Outer Broad, particularly in the hemidythal zone.

Ceramium rubrum (Huds.) Agardh. Common in the eudythal and in part in the hemidythal zone in the whole area of the fjord.

Ceramium tenuissimum (Lyngb.) J. Agardh. Present in the eudythal zone in the greater part of the fjord.

Chantransia sp. found as an epiphyte in both the Outer and the Inner Broad.

Chondrus crispus (L.) Stackh. Common in the eudythal zone in the entrance area. On the Hundested pier in the hemidythal zone. Otherwise found only in the bight of Nykøbing.

Corallina officinalis L. Found at a depth of 9 m. in the entrance area.

Delesseria sanguinea (L.) Lamouroux. In May and June generally the dominant species in the lower part of the eudythal zone in the entrance area. In July it has lost the leafy parts of its thallus in this area. The species does not enter the Outer Broad.

Dumontia filiformis (O. Fr. Müll.) Grev. Observed in the spring and early summer in the Outer and the Inner Broad.

Furcellaria fastigiata (Hudson) Lamouroux. One of the quantitatively most important algae in the eudythal zone in the whole Isefjord complex. It is also found in the hemidythal zone except in the entrance area.

Hildenbrandia prototypus Nardo. Found on stones in the hemidythal zone in the entrance area, the Outer and the Inner Broad. The occurrence is, however, rather heterogeneous. Thus it is found in the eastern, but not in the western part of the Inner Broad. The character of the bottom beside the stones is of importance for its occurrence.

Membranoptera alata (L.) Stackhouse. Small amounts found in the eudythal zone in the entrance area.

Nemalion multifidum (Web. et Mohr) J. Ag. In the height of summer found here and there on stones in the hemidythal zone in the fjord area. Prominent only in the Outer Broad.

Phyllophora Brodiaei (Turn.) J. Ag. Found in the eudythal zone (may enter the hemidythal zone) in the entrance area, the Outer and Inner Broad, and the outer part of the Roskilde Fjord.

Phyllophora membranifolia (G. & W.) J. Ag. Found in the eudythal zone in the entrance area.

Polyides rotundus (Gmel.) Grev. A single specimen found at a depth of 5 m. in the northern part of the Roskilde Fjord.

Polysiphonia elongata (Huds.) Harvey. Found in the eudythal zone in the whole Isefjord area. Prominent only in the entrance area.

Polysiphonia nigrescens (Engl. Bot.) Grev. Considerable amounts found in the whole fjord area. Especially observed in the eudythal zone, but also enters the hemidythal zone.

Polysiphonia violacea (Roth.) Grev. Found in the eudythal zone in the whole fjord area. May also be found in the hemidythal zone.

Porphyra leucosticta Thuret. Found on the pier at Hundested. Hagerup 1946 states having found small specimens of *Porphyra umbilicalis* (L.) on the outside of the pier. No doubt the species in question was *P. leucosticta.*

Rhodomela subfusca (Woodw.) Agardh. The species was found in the eudythal zone in all subareas except the Holbæk Fjord.

Phaeophyceae.

Chorda Filum (L.) Stackh. Whereas only small amounts of this plant were found in the entrance area, and only below a depth of about 5 m., considerable quantities are found both in the hemidythal and the eudythal zone in the other areas of the fjord complex. The species is not very sensitive to pollution.

Chordaria flagelliformis (Müll.) Ag. Found in the hemidythal zone in the entrance area and in the outer part of the Outer Broad.

Chaetopteris plumosa (Lyngb.). Found in the Inner Broad off Bognæs.

Dictyosiphon foeniculaceus (Huds.). Found only in the Outer Broad.

Ectocarpus confervoides (Roth.) Kjellm. This variable species was common in the eudythal zone in the entrance area, the Outer and the Inner Broad, and the outermost part of the Roskilde Fjord.

Elachista fucicola (Vell.) Aresch. Found on *Fucus* in the Outer Broad.

Fucus serratus L. Characteristic of the upper part of the eudythal zone. Only on the pier at Hundested it entered the hemidythal zone (see further on p. 81). The species is absent from the Holbæk Fjord and the inner part of the Roskilde Fjord.

Fucus spiralis L. Found around the mean level of the sea at Lynæs harbour and at Rørvig.

Fucus vesiculosus (L.). Dominant in the hemidythal and the upper part of the eudythal zone in the whole fjord complex.

Halidrys siliquosa (L.). One of the dominant species in the upper part of the eudythal zone in the Outer Broad. It was not found at all in the Inner Broad and in the Roskilde Fjord. In the entrance area it was not found until at a depth of 5 m.

Laminaria digitata (L.). A single specimen was found on a *Modiola* at a depth of 9 m. in the entrance area.

Leathesia difformis (L.) Aresch. This epiphyte was found at depths of 1—5 in the Outer Broad.

Petalonia Fascia (O. F. Müll.) Kuntze. Found on the south pier at Hundested in the summer of 1943, but not in the summer of 1944.

Pylaiella litoralis (L.) Kjellm. Observed in the Outer Broad and in the Roskilde Fjord, but no doubt occurs in the whole of the fjord area. The species was found by Rosenvinge in the Holbæk Fjord.

Ralfsia verrucosa (Aresch.). Common in many places in the hemidythal zone in the whole of the fjord area. Was observed right into the head of the Lejrevig.

Scytosiphon Lomentaria (Lyngb.). Was found in the hemidythal zone in the Outer Broad, the Inner Broad, and the outer part of the Roskilde Fjord.

Sphacelaria bipinnata Sauv. On *Halidrys* in the Outer Broad.

Sphacelaria cirrosa (Roth.). Particularly on *Fucus* in the Outer Broad. Was also found in the Inner Broad and the Roskilde Fjord.

Sphaerotrichia divaricata (Ag.) Kylin. Found in the Inner and the Outer Broad at depths of 1—1.5 m.

Stilophora rhizoides (Ehrb.) J. Ag. Common in the height of summer on *Fucus* in the Outer Broad. Has also been found in the Inner Broad.

Stilophora tuberculosa (Hornem.) Rke. Observed in the Outer Broad.

Striaria attenuata Grev. Found in the eudythal zone in the Outer Broad as well as the Inner Broad.

Chlorophyceae.

Bryopsis plumosa (Huds.). Found in the hemidythal zone on the pier at Hundested.

Chaetomorpha aerea Kütz. Found in protected places in the Outer Broad, the Inner Broad, and the outer part of the Roskilde Fjord.

Chaetomorpha Melagonium (W. et M.). Found on the pier at Hundested.

Chaetomorpha Linum (Fl. Dan.). Found in the whole of the fjord area, particularly in the Roskilde Fjord.

Cladophora sericea (Huds.). Found in the whole of the fjord area, about July 1st in huge detached masses.

Cladophora sp. sp. Various other species of *Cladophora* not determined are found in the fjord.

Enteromorpha sp. sp. Species of this genus are distributed in the whole of the fjord area and quantitatively considerable amounts may be found.

Monostroma Grevillei Thur. Common in the hemidythal zone of sheltered localities in spring.

Monostroma Wittrockii. Found on the pier at Ejby.

Pringsheimia scutata. The Inner Broad.

Ulothrix implexa. The Inner Broad.

Urospora sp. On the bridge embankment at Frederikssund.

Ulva lactuca (L.). Attached on piers at Hundested and Lynæs. In a detached form in the Holbæk Fjord and the Roskilde Fjord.

Cyanophyceae.

Calothrix scopulorum (W. et Mohr). Found in the adythal zone and the upper part of the hemidythal zone, particularly on piers.

Lyngbya aestuarii (Mert). Found on the beach off the farm of Grønnæsse at the entrance to the Roskilde Fjord. Together with the following species it forms coherent films.

Microcoleus chtonoplastes (Hofm.-Bang). Found together with the preceding species.

Rivularia atra Roth. Found in the hemidythal zone except in the Holbæk Fjord.

Angiospermae.

Potamogeton pectinatus L. Common in the Roskilde Fjord at depths from 0.4 m. to 4 m. Was also observed in Tempelkrog (the Inner Broad). The species was previously found by Rosenvinge in the Outer Broad, south of Rørvig.

Ruppia maritima L. The low form of *Ruppia* in the Isefjord area has been determined as this species. It was, however, generally found in a sterile state. It occurs in the whole area of the fjord with the exception of the entrance.

Ruppia spiralis (L.) Dumort. Found together with the preceding species. It is slightly taller, occurs at slightly greater depths (down to 2 m.), and is fertile in the height of summer.

Zostera Hornemanniana Tutin. Found in the hemidythal zone in the whole area with the exception of the entrance.

Zostera marina L. Found in the whole fjord complex to a depth of 5 m. (in the entrance area found at a depth of 9 m.). While in 1943 the species had regenerated completely after the grass-wrack disease in the interior parts of the area, this was not the case in the Outer Broad and the entrance area.

Zostera nana Roth. The species was found in the upper part of the hemidythal zone in protected places where the bottom was not soft, in the Outer and the Inner Broad, and in the Roskilde Fjord.

Zannichellia palustris L. Common in the whole of the Roskilde Fjord from the hemidythal zone to a depth of 6 m. The species was also found in a few places in the Outer Broad. Its absence in the Inner Broad and in the Holbæk Fjord was due to the salinity which was a little too high there.

Chapter Seven

TABLES OF THE BENTHOS VEGETATION

A. The Entrance Area (Area I).

Table 20.

St. Ia. Off Spodsbjerg Lighthouse. 28.5.1941.

Near and above the mean level of the sea no large algae. *Fucus vesiculosus* from about — 0.3 m. Stony beach.

At depths of 1.5—2 m. Big stones.

Dominant:
- *Fucus vesiculosus*
- *Fucus serratus* (at a depth of 2 m. larger amounts than *F. vesiculosus*).

Considerable amounts:
- *Furcellaria fastigiata*
- *Phyllophora Brodiaei*
- *Ahnfeltia plicata*
- *Polysiphonia nigrescens*
- *Ceramium rubrum*
- *Chondrus crispus.*

Present:
- *Enteromorpha (intestinalis?).*

At depths of 3—4 m. Big stones.

Dominant:
Fucus serratus
Furcellaria fastigiata.
Considerable amounts:
Ceramium rubrum.
Present:
Delesseria sanguinea
Membranoptera alata
Phyllophora Brodiaei
Polysiphonia violacea
Polysiphonia nigrescens
Fucus vesiculosus
Cladophora sp. low.

At a depth of 6 m.

Dominant:
Furcellaria fastigiata
Delesseria sanguinea.
Considerable amounts:
Phyllophora Brodiaei
Ceramium rubrum.
Present:
Fucus serratus
Fucus vesiculosus
Chorda filum
Ahnfeltia plicata
Polysiphonia violacea
Phyllophora membranifolia
Ectocarpus confervoides (on *Phyllophora*).

At a depth of 8 m. Pure sand.

No plants.

At a depth of 9 m. (a slightly more northerly position). Sand with a few scattered stones.

Dominant:
Fucus serratus
Furcellaria fastigiata
Delesseria sanguinea.
Considerable amounts:
Phyllophora Brodiaei
Phyllophora membranifolia
Ceramium rubrum
Polysiphonia elongata
Polysiphonia violacea.

Present:

Fucus vesiculosus
Laminaria digitata (on *Modiola*)
Polysiphonia nigrescens
Chondrus crispus
Corallina officinalis
Callithamnion sp. (on *Polysiphonia*)
Zostera marina (one specimen with leaves 10 cm long).

According to Rosenvinge's journals the following species, not observed in May 1941, were found in July 1892: *Brongniartella byssoides, Epilithon membranaceum* (on *Furcellaria*), *Petrocelis Hennedyi, Polyides rotundifolia.*

Rather considerable quantities of *Halidrys siliquosa* were found at supplementary collections at St. Ia on June 5th, 1943, at a depth of 5 m.

Table 21.

St. Ib. The outside of the southern pier, Hundested harbour, 10 m. from the pier-head. The pier, which is built as a breakwater of big stones, here faces the west. 6.8.1944. Examined by Mr. S. Lund, M. Sc.

+ 100 — + 13 cm.

Calothrix scopulorum (no coherent carpet).

+ 13 — 0 cm.

Calothrix scopulorum (forming a coherent carpet with other blue algae and diatoms)
Porphyra leucosticta (small patches at about + 13 cm.)
Enteromorpha sp. (upper limit + 8 cm.); common
Cladophora sericea (upper limit + 8 cm.); present
Nemalion multifidum (upper limit + 8 cm.); present.

0 — — 7 cm.

Enteromorpha sp. dominant
Cladophora sericea; dominant
Calothrix scopulorum; present down to — 3 cm.
Ceramium diaphanum; considerable amounts, faded
Ceramium rubrum; present, faded
Nemalion multifidum; present
Hildenbrandia prototypus; present
Callithamnion corymbosum; present.

- 7 — — 50 cm.

Ceramium diaphanum; dominant, not faded
Polysiphonia nigrescens; dominant
Polysiphonia violacea; present
Chordaria flagelliformis; present
Chordaria crispus; present
Chaetomorpha Melagonium; present
Bryopsis plumosa (upper limit — 30 cm.)

Fucus vesiculosus (upper limit — 30 cm.)
Fucus serratus (upper limit — 30 cm.).

— 50 — — 200 cm.
Fucus vesiculosus; dominant
Fucus serratus; dominant.

Below — 200 cm. Bare sandy bottom.

A narrow fringe of *Petalonia Fascia* was found at a depth of about 10 cm. in July 1943. Because of the weather conditions a thorough examination of the locality was impracticable. Minor amounts of *Ulva lactuca* were found at depths of about 15—50 cm.

Table 22.

St. Ic. Off Skansehage. 8.6.1942.

At depths of 0.3—1 m. Sandy beach with many pebbles, on which

Dominant:
Fucus vesiculosus.
Present:
Ralfsia verrucosa
Rivularia atra
Enteromorpha sp.

At depths of 2—3 m. Scattered, particularly smaller, stones on sandy bottom.

On sand small amounts of *Zostera marina* (leaves 9—15 long, 3 mm. broad).
On stones:
Dominant:
Fucus vesiculosus
Fucus serratus
Furcellaria fastigiata.
Considerable amounts:
Ceramium rubrum
Polysiphonia nigrescens
Polysiphonia violacea
Rhodomela subfusca
Phyllophora Brodiaei
Phyllophora membranifolia
Ectocarpus confervoides (on *Fucus*).
Present:
Ceramium tenuissimum.

At a depth of 5 m. Scattered stones on sandy bottom.

On sand small amounts of *Zostera marina.*
On stones:
Dominant:
Fucus serratus
Furcellaria fastigiata.

Considerable amounts:
Delesseria sanguinea
Ahnfeltia plicata
Polysiphonia nigrescens
Phyllophora Brodiaei
Phyllophora membranifolia
Chondrus crispus
Ectocarpus confervoides (on *Fucus*).
Present:
Fucus vesiculosus
Chorda filum
Membranoptera alata
Rhodomela subfusca.

At depths of 7—8 m. Single stones on sandy bottom (little plant material in the dredge).

Present:
Furcellaria fastigiata
Ceramium rubrum
Ahnfeltia plicata
Phyllophora sp.
Chorda filum
Fucus vesiculosus
Ectocarpus confervoides (on *Fucus*).

B. The Outer Broad (Area II).

Table 23.

St. IIa. Off Carlsminde. 9.7.1941 (the determinations from 0—0.5 m. made on 30.7.1943 at a slightly more westerly position—between Carlsminde and Lynæs harbour.

At depths of 0—0.5 m. Sandy bottom mixed with clay, with some small and a few big stones.

On soft bottom:
Zostera nana (from — 5 cm.); scattered minor growths
Ruppia spiralis (from — 15 cm.); large growths, fructifying
Ruppia marina (from — 15 cm.); some sterile plants probably of this species
Zostera Hornemanniana (from — 20 cm.); scattered growths.
On stones:
Fucus vesiculosus (from — 10 cm.); large amounts
Ceramium (presumably *C. diaphanum*); large amounts on *Fucus*
Ralfsia verrucosa (from — 10 cm.); common
Rivularia atra (from — 10 cm.); common.
Enteromorpha sp. (small); small amounts, but occurring everywhere (from — 10 cm.).
(On 20.5.1941 *Scytosiphon lomentaria* and *Monostroma Grevillei* were found there).

At a depth of 1 m. Rather big stones.

Dominant:
Fucus vesiculosus.

Considerable amounts:
Fucus serratus
Furcellaria fastigiata
Chorda filum
Chordaria flagelliformis
Elachista fucicola (on *Fucus*).
Present:
Ceramium rubrum
Polysiphonia nigrescens
Leathesia difformis (on *Furcellaria*)
Stilophora rhizoides (on *Fucus*)
Phyllophora sp.

At a depth of 2 m. Rather large stones (on sand among stones small amounts of *Zostera marina*).

Dominant:
Fucus serratus.
Considerable amounts:
Halidrys siliquosa
Chorda filum
Furcellaria fastigiata
Ceramium rubrum (particularly as an epiphyte).
Present:
Fucus vesiculosus
Phyllophora Brodiaei
Polysiphonia nigrescens
Ceramium tenuissimum
Ahnfeltia plicata
Cladophora sericea
Stilophora rhizoides (on *Fucus*)
Elachista fucicola (on *Fucus*).

At a depth of 4 m. Rather big stones.

Dominant:
Halidrys siliquosa
Chorda filum
Furcellaria fastigiata.
Considerable amounts:
Fucus serratus
Ceramium rubrum
Sphacelaria (prob. *S. cirrosa*); on *Fucus.*
Present:
Polysiphonia nigrescens
Rhodomela subfusca
Phyllophora Brodiaei
Cladophora sericea.

At a depth of 6 m. Single stones (few algae in the dredge).

Chorda filum
Furcellaria fastigiata
Phyllophora sp.
Ceramium rubrum
Cladophora sericea.

At a depth of 7.5 m. Soft bottom, presumably without stones.
Chorda filum (1 specimen)
Cladophora sericea (very small amount).

Table 24.

St. IIb. The outside of the western pier (breakwater of big stones), Kulhus harbour. 1.8.1943.

+ 25 cm — — 5 cm.
Calothrix scopulorum
Rivularia atra (from + 10 cm.)
Ralfsia verrucosa (from 0 cm.).

— 5 cm. — — 75 cm.
Rivularia atra (lower limit — 50 cm.)
Ralfsia verrucosa (lower limit about — 50 cm.)
Nemalion multifidum (fringe at about — 15 cm.)
Chordaria flagelliformis (upper limit — 25 cm.)
Fucus vesiculosus (upper limit of very young plants — 20 cm, of older plants —50 cm.)
Ceramium (probably particularly *C. diaphanum*) (upper limit — 30 cm.).

Table 25.

St. IIc. The beach southwest of Kulhus harbour (sandy beach with big stones). 1.8.1943.

On stones below about — 15 cm.:
Fucus vesiculosus; particularly young individuals
Nemalion multifidum; large amounts
Chorda filum; a few specimens
Stilophora rhizoides; most important epiphyte on *Fucus*
Rivularia atra
Ralfsia verrucosa.
On sand a few specimens of *Zostera Hornemanniana.*

Table 26.

St. IId. The outside of the eastern pier in Lynæs harbour. Big stones, from 0.3 m. sandy bottom with big and small stones.

Vegetation very much like that at St. IIb; still *Fucus spiralis* was found at + 5 cm. — 15 cm. Furthermore *Chaetomorpha aerea, Hildenbrandia prototypus,* and *Ulva lactuca* (attached) were observed. Particularly large amounts of *Fucus spiralis* were found on the inside of the breakwater (continuation of the western pier), but not on its outside.

Table 27.

St. IIe. Alholm reef (no investigations above a depth of 1.5 m.). 9.7.1941.

At a depth of 1.5 m. Sandy bottom with scattered, in part big, stones.

On sand rather large amounts of *Zostera marina* with admixture of a few specimens of *Zannichellia palustris.*

On stones:

Dominant:

Fucus vesiculosus
Fucus serratus.

Considerable amounts:

Chorda filum
Halidrys siliquosa
Cladophora sericea.

Present:

Rhodomela subfusca
Polysiphonia nigrescens
Polysiphonia violacea
Ahnfeltia plicata
Ceramium rubrum.

Old parts of *Fucus* (particularly *F. vesiculosus*) greatly overgrown with: *Ectocarpus, Sphacelaria, Elachista fucicola, Ceramium,* and *Stilophora rhizoides.*

At a depth of 3 m. Sandy bottom with scattered stones (on sand some *Zostera marina*).

On stones:

Dominant:

Fucus serratus
Furcellaria fastigiata.

Considerable amounts:

Chorda filum
Ceramium rubrum
Rhodomela subfusca
Phyllophora Brodiaei.

Present:

Cladophora sericea
Polysiphonia violacea.

Old parts of *Fucus serratus* overgrown with *Elachista fucicola,* and *Ectocarpus.*

At depths of 6—7 m. Sandy bottom with a few scattered stones (no plants on sand).

On stones:

Dominant:

Furcellaria fastigiata.

Considerable amounts:

Ceramium rubrum
Chorda filum
Cladophora sericea.

Present:
Fucus serratus (with *Elachista fucicola*)
Phyllophora sp.

At a depth of 9 m. No stones, no plants.

Table 28.

St. IIf. Off Nakke Hage (no investigations above a depth of 1 m.). 25.5.1941.

At depths of 1—1.5 m. Stones.

Dominant:
Fucus vesiculosus
Fucus serratus.
Considerable amounts:
Furcellaria fastigiata
Ahnfeltia plicata
Polysiphonia nigrescens
Dumontia incrassata
Dumontia filiformis
Ceramium rubrum.
Present:
Ceramium sp.
Halidrys siliquosa.

At depths of 2—2.5 m. Stones.

Dominant:
Halidrys siliquosa.
Considerable amounts:
Fucus serratus
Furcellaria fastigiata
Ceramium rubrum.
Present:
Fucus vesiculosus
Phyllophora Brodiaei
Polysiphonia nigrescens.

At depths of 3—4 m. Stones (between stones small amounts of *Zostera marina*).

Dominant:
Halidrys siliquosa
Furcellaria fastigiata.
Considerable amounts:
Rhodomela subfusca
Phyllophora (*Brodiaei*?).
Present:
Fucus serratus
Chorda filum

Ectocarpus confervoides
Ceramium rubrum
Cladophora sericea
Chantransia sp. (on *Ectocarpus*).

At a depth of 6 m. Stones.

Dominant:
Furcellaria fastigiata.
Considerable amounts:
Rhodomela subfusca
Phyllophora (*Brodiaei*?).
Present:
Fucus serratus
Halidrys siliquosa
Ectocarpus siliculosus
Ceramium rubrum
Polysiphonia nigrescens
Chantransia sp.
Cladophora sericea.

At depths of 8—9 m. A few stones (little plant material in the dredge).

Present:
Furcellaria fastigiata
Fucus serratus
Ectocarpus siliculosus
Ceramium rubrum
Ceramium sp.
Polysiphonia nigrescens.

Table 29.

St. IIg. Nykøbing Bight off Ringholm (no investigations above a depth of 2 m.). 8.6.1942.

At a depth of 2 m. Many stones.

Dominant:
Fucus serratus
Fucus vesiculosus
Furcellaria fastigiata.
Considerable amounts:
Polysiphonia nigrescens
Polysiphonia violacea
Phyllophora Brodiaei
Chondrus crispus
Ahnfeltia plicata
Dumontia filiformis
Dictyosiphon foeniculaceus

Chorda filum
Cladophora sp.

Present:

Cladophora sericea.

Epiphytically on *Fucus* (particularly *F. vesiculosus*): *Pylaiella, Sphacelaria, Ectocarpus,* and *Polysiphonia.*

Epiphytically on *Phyllophora*: *Leathesia difformis.*

At a depth of 5 m. A few stones. On soft bottom *Zannichellia palustris* and *Zostera marina.*

Dominant:

Chorda filum.

Present:

Fucus serratus
Polysiphonia nigrescens
Ceramium rubrum
Rhodomela subfusca
Phyllophora Brodiaei
Ahnfeltia plicata
Cladophora sericea.

Table 30.

St. IIh. Nykøbing Bight, slightly east of embankment. 13.8.1943.

The foreshore has a sandy bottom mixed with a little clay and with many small and a few big stones.

On stones:

Chaetomorpha aerea (a little below the mean level of the sea)
Cladophora sp. (a little below the mean level of the sea)
Fucus vesiculosus (from about — 25 cm.); large amounts
Chorda filum.

On sand:

Ruppia (*maritima*?); rather large populations
Zostera Hornemanniana; small amounts.

Table 31.

St. IIi. Nykøbing harbour, 50 m. from outlet of main sewer. 13.8.1943.

About the main level of the sea:

Chaetomorpha aerea; large amounts
Enteromorpha sp.

From a depth of about 0.5 m.:

Chorda filum; large amounts

(Immediately off the outlet of the sewer no *Chorda*).

Table 32.

St. IIj. Off Nissebakker, Hornsherred. 1.8.1943.

Sandy beach with many big and small stones.
On sand:
Zostera Hornemanniana; a fair amount.
On stones from somewhat below the main level of the sea:
Fucus vesiculosus
Nemalion multifidum
Rivularia atra
Ralfsia verrucosa.

Table 33.

St. IIk. The bight off Jægerspris. 1.8.1943.

Sandy beach, shallow far out.
Ruppia (low form; *R. maritima*?); large growths
Zostera Hornemanniana; sporadic
Zostera nana; sporadic
Enteromorpha sp.

Table 34.

St. III. Næsby reef. 24.6.1941.

At depths of 1—1.5 m. Sandy bottom with many stones.

On sand:
Zostera marina; large growths.
On stones:
Dominant:
Fucus vesiculosus
Fucus serratus
Halidrys siliquosa.
Considerable amounts:
Furcellaria fastigiata
Polysiphonia nigrescens
Phyllophora Brodiaei
Chorda filum
Ahnfeltia plicata
Cladophora sericea (detached).
Present:
Ceramium rubrum
Rhodomela subfusca
Sphaerotrichia divaricata.

Fucus (particularly *F. vesiculosus*) densely overgrown with *Elachista fucicola, Sphacelaria, Pylaiella, Ectocarpus,* and *Stilophora rhizoides.*

At a depth of 2.5 m. Sandy bottom with many stones (on sand small amounts of *Zostera marina*).

Dominant:
Fucus serratus
Halidrys siliquosa
Furcellaria fastigiata.
Considerable amounts:
Chorda filum
Phyllophora
Ceramium rubrum (particularly as an epiphyte)
Ahnfeltia plicata
Cladophora sericea (detached).
Present:
Polysiphonia nigrescens
Fucus vesiculosus.
Fucus densely overgrown (nearly exclusively with *Sphacelaria cirrosa*).
Furcellaria and *Ahnfeltia* densely overgrown with *Leathesia difformis.*

At depths of 4—5 m. A good number of stones (*Zostera* not observed).

Dominant:
Furcellaria fastigiata
Ceramium rubrum.
Considerable amounts:
Chorda filum
Phyllophora sp.
Cladophora sericea (detached).
Present:
Fucus serratus
Rhodomela subfusca
Ceramium tenuifolium
Striaria attenuata
Leathesia difformis (on *Furcellaria*).

At depths of 6—7 m.

Considerable amounts:
Polysiphonia nigrescens
Furcellaria fastigiata
Phyllophora sp.
Present:
Rhodomela subfusca
Ceramium rubrum
Striaria attenuata.

At a depth of 9 m. A few stones (little material of algae in the dredge).

Furcellaria fastigiata
Polysiphonia nigrescens
Phyllophora sp.
Striaria attenuata.

C. The Inner Broad (Area III).

Table 35.

St. IIIa. Off Bognæs. 24.6.1941.

At depths of 0—1 m. Sand with rather big stones.

On sand:

Small amounts of *Ruppia* and *Zostera nana* from a little below the mean level of the sea.

On stones:

Fucus vesiculosus.

At a depth of 1.5 m. Sand with rather big stones.

On sand:

Large growths of *Zostera marina* with admixture of small amounts of *Ruppia spiralis.*

On stones:

Dominant:

Fucus serratus
Chorda filum
Furcellaria fastigiata.

Considerable amounts:

Polysiphonia nigrescens
Cladophora sericea (detached).

Present:

Fucus vesiculosus
Rhodomela subfusca
Chaetopteris plumosa
Ceramium tenuissimum.

Epiphytes: *Sphacelaria cirrosa* (on *F. vesiculosus*), *Chantransia* sp., *Pringsheimia scutata.*

At a depth of 2.5 m. Sand with rather big stones (on sand considerable amounts of *Zostera marina*).

On stones:

Dominant:

Fucus serratus
Chorda filum
Furcellaria fastigiata.

Considerable amounts:

Rhodomela subfusca
Cladophora sericea (detached).

Present:

Ceramium rubrum
Ceramium tenuissimum
Polysiphonia nigrescens
Phyllophora Brodiaei
Striaria attenuata.

At depths of 4—4.5 m. Very few stones (on soft bottom no attached plants).

Dominant:
Polysiphonia nigrescens.
Considerable amounts:
Furcellaria fastigiata
Chorda filum (particularly on shells).
Present:
Ceramium rubrum
Phyllophora Brodiaei
Fucus vesiculosus
Callithamnion sp.
Cladophora sericea (detached)
Polysiphonia violacea.

At a depth of 6 m. Soft bottom. A few detached plants.

At a depth of 8 m. Soft bottom. Some detached plants.

At a depth of 14 m. Soft bottom. No plants.

Table 36.

St. IIIb. Udby Vig, southern part. 27.7.1941.

Sandy bottom (with little admixture of mud). On the shallow bottom, which stretches far out, large growths of *Ruppia,* with admixture of *Zostera Hornemanniana* and *Zostera nana.* On the beach algae cast ashore, particularly *Cladophora sericea.*

Table 37.

St. IIIc. Dronningdyssen. 9.7.1941.

At a depth of 1.5 m. Scattered stones (beside the stones some *Zostera marina*).

On stones:
Dominant:
Fucus serratus
Fucus vesiculosus
Chorda filum (also on shells).
Considerable amounts:
Sphaerotrichia divaricata
Polysiphonia nigrescens
Cladophora sericea (detached).
Present:
Ceramium rubrum (particularly on *Zostera*)
Ceramium tenuissimum (particularly on *Zostera*).

At a depth of 3 m. Scattered stones (beside the stones considerable amounts of *Zostera marina*).

On stones:
Dominant:
Fucus serratus
Polysiphonia nigrescens.
Considerable amounts:
Chorda filum
Cladophora sericea.
Present:
Polysiphonia violacea
Ceramium rubrum (particularly on *Zostera*)
Ceramium tenuissimum (particularly on *Zostera*).

At depths of 4—5 m. A few small stones (on soft bottom small amounts of *Zostera marina*).

On stones:
Present:
Chorda filum
Polysiphonia violacea.

At a depth of 7 m. Quite soft bottom (no *Zostera*).

Very small amounts of detached algae were dredged:
Furcellaria fastigiata
Ceramium rubrum
Polysiphonia nigrescens
Enteromorpha sp.
Cladophora sericea.

Table 38.

St. IIId. South of the naval station. 24.4.1941 (sandy bottom investigated on 30.9.1941).

About — 10 — — 50 cm. Sandy bottom a little admixture of organic matter. Many small stones, a few bigger ones.

On stones:
Fucus vesiculosus (only on big stones)
Furcellaria fastigiata
Phyllophora Brodiaei
Dumontia filiformis
Scytosiphon lomentarius
Polysiphonia nigrescens
Monostroma Grevillei.

From a depth of about 1 m.: *Fucus serratus.*

On sandy bottom uppermost *Ruppia* and *Zostera Hornemanniana.* From a depth of 0.5 m. vigorous growths of *Zostera marina.*

On heap of stones at the naval station *Ceramium* sp. and *Cladophora glaucescens* at — 25 cm. Small amounts of *Nemalion multifidum* observed in July.

Table 39.

St. IIIe. The beach in Vellerup Vig (100 m. within jetty). 24.8.1943.

Firm sandy bottom with many small stones and a few somewhat bigger ones (fresh-water oozes out).

On sand from about — 30 cm.

Dominant:

Ruppia.

In patches here and there: *Zostera nana* and *Zostera Hornemanniana.*

On stones:

Considerable amounts:

Enteromorpha intestinalis (about 0 cm, other species farther down)
Hildenbrandia prototypus
Fucus vesiculosus
Chaetomorpha aerea
Polysiphonia nigrescens
Rivularia atra.

Present:

Chorda filum
Ralfsia verrucosa.

Table 40.

St. IIIf. The outside of the pier at Ejby harbour (about 10 m. from pierhead; big stones. 25.8.1943.

About 50 cm.—about 0 cm.:

Calothrix scopulorum.

About — 20 cm.—about — 35 cm.:

Hildenbrandia prototypus (dominant)
Enteromorpha sp.
Ceramium rubrum
Monostroma Wittrockii
Cladophora sericea.

About — 35 cm.—about — 1 m.:

Fucus vesiculosus (dominant)
Hildenbrandia
Ceramium rubrum (very small amount).

From a depth of 1 m. bare sandy bottom without plants (on sandy bottom north of the harbour there were no plants).

From 0 m. to a depth of 1 m. a few stones with *Fucus vesiculosus.*

Table 41.

St. IIIg. The beach below the Bramsnæsvig Hotel (sand with small stones). 25.8.1943.

On stones from about — 40 cm.:

Hildenbrandia prototypus
Fucus vesiculosus.

On sand from about — 40 cm.:

Zostera marina.

From a depth of about 1 m. *Zostera marina* forms dense meadows, which according to statements by the fishermen are again found in the whole of the creek.

Table 42.

St. IIIh. Tempelkrog off Strandskoven. 25.7.1941.

At depths of about 0.2—0.5 m. (sandy beach with a few stones).

On sand:

Ruppia (at any rate and primarily *R. spiralis*); large growths
Zostera marina (small amounts at the lower limit).

On stones:

Fucus vesiculosus
Enteromorpha (presumably *E. intestinalis*).

Detached:

Large amounts of *Chaetomorpha Linum* and *Cladophora sericea.*

At a depth of 1.5 m. Soft bottom with a few stones.

On soft bottom:

Zostera marina (large amounts)
Ruppia (large amounts).

On stones and shells:

Chorda filum (large amounts)
Enteromorpha (large amounts).

Detached:

Chaetomorpha Linum
Ulothrix implexa
Cladophora sericea
Ceramium rubrum.

At a depth of 2.5 m. Soft bottom with *Zostera marina.* Other species:

Chorda filum (on shells)
Potamogeton pectinatus (one specimen)
Ceramium rubrum
Ectocarpus confervoides (on *Zostera*)
Enteromorpha intestinalis (detached)
Chaetomorpha linum (detached)
Cladophora sericea (detached).

At a depth of 4 m. Soft bottom with small amounts of detached *Chaetomorpha Linum* and *Cladophora sericea.*

Table 43.

St. IIIi. Tempelkrog off Eriksholm. 25.7.1941.

Sandy bottom with great admixture of mud (stinking under the surface). Shallow bottom far out. A few large stones.

Ruppia (large growths)
Fucus vesiculosus (on stones)
Enteromorpha (on stones).

D. The Holbæk Fjord (Area IV).

Table 44.

St. IVa. Off Rønnen. 9.7.1941.

At a depth of 1.5 m. Soft bottom with scattered, not particularly big stones.

On soft bottom:

Zostera marina (large amounts).

On stones:

Considerable amounts:

Chorda filum
Furcellaria fastigiata
Ceramium rubrum (also on *Zostera* and detached).

Present:

Polysiphonia nigrescens
Polysiphonia violacea.

Detached:

Enteromorpha sp.
Cladophora sericea.

At a depth of 2.5 m. Soft bottom with large growths of *Zostera marina.* (Large amounts of detached *Ceramium rubrum,* small amounts of *Enteromorpha* sp.).

At a depth of 4 m. Soft bottom with small amounts of detached *Ceramium rubrum, Enteromorpha* and *Cladophora sericea.*

Table 45.

St. IVb. Off the mouth of Tuse Å. 9.7.1941.

At a depth of 1.5. m, Soft bottom with scattered *Zostera marina* and small amounts of *Ruppia.*

Detached:

Enteromorpha sp. (large amounts)
Furcellaria fastigiata (some)
Ceramium rubrum (some)
Polysiphonia violacea (some)
Polysiphonia nigrescens (some).

Table 46.

St. IVc. The foreshore off Dragerup. 30.9.1941.

At a depth of about 25 cm. soft, muddy bottom, with admixture of small stones.

On soft bottom: small amounts of low *Ruppia* (*R. maritima*?).
On stones: Large amounts of *Enteromorpha.*
Detached: Small *Ulva lactuca.*

At a depth of about 50 cm. Soft bottom with small stones and a few bigger stones.

On soft bottom:

Ruppia spiralis (large growths; fertile)
Ruppia (low; sterile *R. maritima*?)
Zostera Hornemanniana.

On big stones:

Fucus vesiculosus.

Detached:

Ulva lactuca (large amounts)
Ceramium rubrum (large amounts)
(on 25.4.1941 *Monostroma Grevillei* was found there).

Table 47.

St. IVd. The foreshore off the park, west of Holbæk (14.8.1941).

Soft bottom, with admixture of many small stones and a few bigger ones.

Large amounts of *Enteromorpha intestinalis* nearest to the beach.

From a depth of about 25 cm. large growths of *Ruppia* with admixture of small amounts of *Zostera Hornemanniana.* On big stones *Fucus vesiculosus.* Large amounts of *Ceramium rubrum* cast ashore.

E. The Roskilde Fjord (Area V).

Table 48.

St. Va. The foreshore east of Kulhus harbour. 1.8.1943.

Sandy bottom with many small stones and scattered big stones.

On soft bottom below a depth of about 20 cm.:

Ruppia (scattered, large growths)
Zostera Hornemanniana (small amounts)
Zostera nana (small amounts).

On stones:

Enteromorpha (*E. plumosa*?) (about 0 cm.)
Fucus vesiculosus (large amounts below a depth of about 20 cm.)
Nemalion multifidum (large amounts below a depth of about 20 cm.)
Scytosiphon Lomentaria
Polysiphonia nigrescens
Ralfsia verrucosa
Rivularia atra
Chaetomorpha aerea
Polysiphonia violacea (very small amounts).

Table 49.

St. Vb. The bight of Frederiksværk. 9.7.1941.

At a depth of 2 m. Scattered small stones on rather soft bottom.

On soft bottom:

Zostera marina (large meadows) with admixture of small amounts of *Zannichellia palustris.*

On stones:

Dominant:

Chorda filum

Fucus serratus.

Considerable amounts:

Fucus vesiculosus

Cladophora sericea (detached).

Present:

Furcellaria fastigiata

Rhodomela subfusca

Polysiphonia nigrescens

Ceramium rubrum

Sphacelaria sp.

Ectocarpus sp. (epiphytically)

Cyanophyceae (epiphytically, especially on *Rhodomela*).

At a depth of 4 m. Scattered smaller stones on rather soft bottom.

On soft bottom:

Zannichellia palustris (large growths) with small admixtures of *Zostera marina* and *Potamogeton pectinatus.*

On stones:

Considerable amounts:

Ceramium rubrum

Polysiphonia nigrescens

Chorda filum.

Present:

Rhodomela subfusca

Ectocarpus sp. (epiphytically)

Cladophora sericea (detached)

Cyanophyceae (epiphytically).

At a depth of 6 m. Soft bottom, presumably with a few smaller stones (little material in dredge).

Zannichellia palustris

Chorda filum

Polysiphonia nigrescens

Polysiphonia elongata

Nostoc — colony

Cyanophyceae (epiphytically).

Table 50.

St. Vc. Off Brovig. 9.6.1942.

At a depth of 2 m. Soft bottom with very few stones.

On soft bottom:
Dominant:
Zostera marina
Ruppia spiralis.
Present:
Zannichellia palustris.
On stones:
Present:
Fucus vesiculosus
Fucus serratus
Polysiphonia nigrescens
Pylaiella littoralis
Cladophora sericea (detached)
Enteromorpha sp. (detached).

At a depth of 3 m. Soft bottom without stones.

Dominant:
Zannichellia palustris.
Present:
Zostera marina
Cladophora sericea (detached).

At a depth of 5 m. Soft bottom with a few stones.

On soft bottom:
Zostera marina (some).
On stones:
Ceramium rubrum
Polysiphonia nigrescens
Phyllophora Brodiaei
Furcellaria fastigiata
Polyides rotunda
Cladophora sericea (detached).

At a depth of 7 m. Soft bottom with dead seaweed. No living plants.

Table 51.

St. Vd. The foreshore at Nedre Draaby. 24.8.1943.

The bottom somewhat muddy with many shells and a few big stones.
Ruppia (low, sterile); dense populations from about — 25 to about — 40 cm.
Ruppia spiralis (high, fertile); dense populations below about — 40 cm.
Fucus vesiculosus (on stones)
Ulva lactuca (detached)
Chaetomorpha Linum (detached).

Table 52.

St. Ve. Off Øksneholm. 8.6.1942.

At a depth of 2 m. Soft bottom with a few stones.

On soft bottom:

Zostera marina (large meadows)
Potamogeton pectinatus (some).

On stones:

Rhodomela subfusca
Polysiphonia nigrescens
Cladophora sericea (detached).

At a depth of 4 m. Soft bottom with a few stones.

On soft bottom:

Zostera marina (some).

On stones:

Ceramium rubrum
Ceramium tenuissimum (in part as an epiphyte)
Polysiphonia nigrescens
Polysiphonia violacea
Cladophora sericea (detached).

At a depth of 6 m. Soft bottom without stones.

Zostera marina
Ceramium tenuissimum (epiphyte on *Zostera*)
Cladophora sericea (detached)
Ceramium rubrum (detached, faded).

Table 53.

St. Vf. Heap of stones on northern side of bridge embankment at Frederikssund. 24.8.1943.

Urospora sp. (fringe about 0 cm.)
Fucus vesiculosus (from about — 25); large amounts
Cladophora sp. (from about — 25 to, at any rate, — 70 cm.); large amounts
Chaetomorpha aerea; the same.

(In the corner towards Hornsherred large masses of algae cast ashore and rotting, with sulphur bacteria).

Table 54.

St. Vg. Off Kølholm. 9.6.1942.

On old oyster shells at depths of 1—2 m.: *Chorda filum* and detached *Cladophora sericea*.

Table 55.

St. Vh. Off Horsehage. 9.6.1942.

At a depth of 2 m.

Soft bottom:

Zostera marina (large meadows)
Potamogeton pectinatus (considerable amounts)
Zannichellia palustris (considerable amounts).

At a depth of 5 m.

Soft bottom:

Zostera marina (considerable amounts)
Cladophora sericea (detached)
Chaetomorpha Linum (detached)
Polysiphonia violacea (fragment).

Table 56.

St. Vi. Off Bognæs. 9.6.1942.

At a depth of 2 m. Soft bottom with *Zostera marina* and small amounts of *Cladophora sericea*.
At a depth of 4 m. Shells; no plants.

Table 57.

St. Vj. Off St. Hans Hospital.

At a depth of 2 m. Many small stones.

Dominant:

Ulva lactuca
Enteromorpha sp. (delicate).

Present:

Polysiphonia nigrescens
Zannichellia palustris
Cladophora sericea (detached).

Table 58.

St. Vk. The foreshore off the wood of Boserup. 11.6.1942.

Rather muddy bottom with scattered stones.

Ruppia (some)
Zostera nana (very small amounts)
Fucus vesiculosus
Ulva lactuca
Enteromorpha sp.
Cladophora sericea (detached).

Table 59.

St. Vl. The foreshore off the Youth Camp, Lejre Vig. 25.8.1943.

Sandy beach with a few small stones (on which *Fucus vesiculosus* and *Ralfsia verrucosa*).

From — 25 to — 40 cm.:

Ruppia spiralis (dense populations)
Ruppia (low, sterile *R. maritima*?) (dense populations)
Zannichellia palustris
Zostera Hornemanniana.

From — 40 to — 60 cm.:

Potamogeton pectinatus.

From — 60 cm.:

Zostera marina (large amounts of detached *Chaetomorpha Linum*).

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DANSK RESUMÉ

I årene 1940—1943 foretog forfatteren, der dengang var assistent ved Planktonlaboratoriet, Kommissionen for Danmarks Fiskeri- og Havundersøgelser, en undersøgelse af planktonproduktionen i Isefjorden. I forbindelse hermed blev også foretaget en undersøgelse af den fastsiddende plantevækst i fjorden, ligesom der blev foretaget hydrografiske observationer af almen og mere speciel art. Endvidere blev der samtidig med disse undersøgelser også foretaget undersøgelser over vegetationen langs Isefjordens kyster. Et arbejde herover er publiceret af Mikkelsen 1949, ligesom et arbejde over de egentlige dyriske planktonorganismer er publiceret af Jespersen 1949. Et arbejde over bunddyrenes planktonlarver vil blive publiceret af G. Thorson. I det foreliggende arbejde fremlægges alt det øvrige materiale.

Kap. 1 omhandler fjordkompleksets hydrografi, herunder også topografi. Der bliver gjort rede for saltholdighed og temperatur, ligesom vandudvekslingen i fjordkomplekset på grundlag af ovennævnte materiale i forbindelse med bestemmelser over nedbørsområdet behandles. På grundlag af de daglige målinger over saltholdigheden ved Frederikssund i Roskilde Fjord 1895—1936 og de samtidigt foretagne målinger over nedbøren i Roskilde Fjords nedbørsområde klarlægges betydningen af svingninger i nedbøren på saltholdigheden i fjorden, hvorved de helt exceptionelt høje saltholdigheder i årene 1939—1942 får deres naturlige forklaring.

Et rigtholdigt materiale af bestemmelser af næringssaltene ammoniak, nitrat, nitrit og fosfat først og fremmest fra Inderbredningen bliver publiceret. Det samme gælder en række bestemmelser over iltforhold og brintjonkoncentration.

Lysforholdene i vandmasserne blev bestemt. Først og fremmest foreligger en undersøgelse foretaget gennem et år i Inderbredningen. Lysets nedtrængningsevne varierer stærkt efter årstid og vejrforhold, ligesom også det relative forhold mellem nedtrængningsevnen for de forskellige lysfarver varierer. Normalt trængte det grønne lys bedst ned. Lysforholdene i Isefjorden er således, at der på grund af lys overalt kan leve planter på bunden, når man lige ser bort fra de dybere render og huller. Når man alligevel mange steder har arealer af havbunden, hvor der ikke findes makroskopiske planter, skyldes dette bundens beskaffenhed.

Kap. 2 omhandler planteplanktonets stofproduktion, der var det centrale emne ved undersøgelserne. Næringssaltenes kredsløb i fjorden behandles derfor også mere indgående på dette sted. Hovedkilden for næringssaltene findes i fjorden selv, idet næringssaltene ved bakteriers virksomhed frigøres fra organiske stoffer, først og fremmest i bunden. Da bakteriernes virksomhed er temperaturafhængig, stiger næringssaltenes frigørelse med temperaturen. Da endvidere næringssaltene med undtagelse af den mørkeste tid om vinteren er begrænsende for planteplanktonets stofproduktion, går sidstnævnte stort set proportionalt med temperaturen. Den mængde af næringssaltene, der årligt tilføres fra land, svarer til den mængde, der årligt går tabt gennem sedimentation og udstrømning af vand fra fjorden.

Stofproduktionen blev målt experimentelt ved at indelukke vand i flasker for 24 timer og ophænge dem i forskellige dybder. Ved hjælp af iltomsætningen, der blev bestemt gennem Winkler-analyser lod det sig beregne, hvor meget organisk stof der blev dannet ved algernes

fotosyntese. Da nogle flasker samtidig var omviklet med lystæt stof, lod det sig også beregne, hvor meget stof der pr. 24 timer blev nedbrudt gennem respirationen.

Stofproduktionsundersøgelserne blev gennemført i 2 år i Inderbredningen; i 1941 blev der i marts til november foretaget bestemmelser 2 gange hver måned, i 1942 blev der kun foretaget bestemmelser een gang hver måned og kun april—august. I fig. 13 er bestemmelserne af fotosyntesen pr. overfladeenhed fremstillet grafisk.

Kurven for 1941 viser, at der i marts samtidig med issmeltningen i fjorden sætter en ret kraftig stofproduktion ind. Stofproduktionen går imidlertid allerede i løbet af april ned på et minimum, idet næringssaltene, der er blevet akkumulerede i løbet af efteråret og vinteren hurtig bliver opbrugt. Først når i maj sommeropvarmningen sætter ind, går stofproduktionen kraftigt igang igen. I begyndelsen af juni indtræder imidlertid et nyt minimum, der skyldes, at larver af blåmuslinger, der nu er fremkommet i vældige masser—ca. 3000 pr. l—holder planteplanktonet nede på et minimum. Stofproduktionen stiger imidlertid hurtigt igen. I juli—september findes det egentlige maksimum for stofproduktionen, der så i løbet af efterårsmånederne igen falder til det absolutte vinterminimum.

Undersøgelserne i 1942 gav samme resultater som i året før. I det følgende år—1943, hvor der ikke blev foretaget egentlige stofproduktionsundersøgelser, men hvor planktonmængden blev bestemt 2 gange om måneden, blev der allerede i begyndelsen af februar påvist et betydeligt planktonmaksimum. Dette skyldes, at der dette år ikke var is i fjorden, således at der allerede så tidligt var lys nok til algernes fotosyntese. På dette tidspunkt var der de to foregående år tyk is med snelag ovenover på hele fjorden. Først da isen og især snelaget begyndte at smelte, kom der tilstrækkeligt lys ned i vandmasserne. Dette skete først i løbet af marts.

Planteplanktonets reelle fotosyntese pr. m.^{2} overflade blev pr. år bestemt til 600 g. kulhydrat, hvilket er omtrent tilsvarende stofproduktionen på en gennemsnits-kornager i Danmark.

Kap. 3 omhandler de kvantitative undersøgelser over planteplanktonet i Isefjorden. I 1940 blev der foretaget undersøgelser både i Inderbredning, Yderbredning og ved indløbet til fjorden på en række togter fra juni til oktober. I årene 1941—1943 blev der kun foretaget undersøgelser i Inderbredningen, men til gengæld hele året rundt.

Forårsmaksimet bestod i alle undersøgelsesårene fortrinsvis af diatomeer. Den typiske "isart" *Detonula confervacea* blev kun fundet i 1941 og 1942, hvor isen dækkede fjorden, derimod ikke i 1943, da dette ikke var tilfældet. Efter forårsmaksimet kommer et typisk minimum, der først i maj afløses af sommermaksimet, der holder sig til hen på efteråret. Sammensætningen af planktonet varierer meget stærkt fra år til år, ikke blot med hensyn til de enkelte arter, men også med hensyn til de store systematiske grupper. De blågrønne algers optræden var især bemærkelsesværdigt. I 1940 fandtes et kraftigt maksimum i højsommeren. I 1941 påvistes de derimod praktisk taget ikke. I 1942 fremkom de blågrønne alger igen i store mængder, medens i 1943 et mindre maksimum blev påvist.

Kap. 4 giver en floristisk oversigt over planteplanktonets arter i Isefjorden. Den vel nok vigtigste stofproducent i Isefjorden *Sceletonema costatum* får en udførlig omtale. Af arter, hvis optræden i Isefjorden er af interesse, kan blandt andet nævnes diatomeerne *Detonula confervacea* og *Asterionella japonica*.

Kap. 5 omhandler den fastsiddende plantevækst i fjordkomplekset. Der blev foretaget undersøgelser i praktisk taget hele området. Der blev foretaget indsamlinger på alle årstider. Det er således muligt at give en oversigt over plantevæksten i alle områderne af fjordkomplekset. Der vises, at sammensætningen af vegetationen er meget afvekslende og årsagerne hertil søges klarlagt.

Forskelligheder i saltholdigheden synes kun at have betydning for et par arter blandt blomsterplanterne, idet *Zannichellia palustris* og *Potamogeton pectinatus* har deres øvre saltholdighedsgrænse ved saltholdigheder, der træffes almindeligt i fjorden. Når disse to arter ikke findes i Inderbredningen (bortset fra Tempelkrog) skyldes det, at saltholdigheden her er lidt for høj.

Temperaturforholdene har stor betydning, idet de høje sommertemperaturer i alle vandmasser i fjorden bevirker, at næsten alle egentlige dybdearter fra Kattegat ikke kan trænge ind i fjorden. Nogle ganske enkelte findes i indløbet til fjorden f. eks. *Delesseria sanguinea*. Allerede tidligt på sommeren, når arten ude i Kattegat lever i bedste velgående, har den i indløbet til fjorden mistet det bladagtige løv — uden tvivl en følge af den for høje temperatur.

Forurening af vandet i fjorden — herunder også selvforurening — spiller en væsentlig — måske den væsentligste — rolle for fordelingen af planterne i fjorden. Brunalgerne *Halidrys siliquosa, Fucus serratus, Fucus vesiculosus* og *Chorda filum* giver en række med stadig stigende tendens til at kunne tåle forurening.

Mangel på kraftigere brænding i de egentlige fjordområder bevirker, at en række alger som f. eks. *Petalonia Fascia* og *Porphyra leucostista* kun findes på molerne i indløbet. Den stærkere brænding her bevirker også, at en art som *Fucus serratus* her går højere op imod overfladen end ellers i fjorden. Denne art tåler kun en mere kortvarig udtørring. Da tidevandet i området kun er ubetydeligt, vil et betydeligt lavvande i fjorden være betinget af storm fra sydøst. Under sådanne betingelser findes der imidlertid brænding i indløbsområdet, hvor der nu vil være dønning. *Fucus serratus* vil derfor ikke blive udsat for udtørring her, selv om den vokser et godt stykke ovenfor lavvandsmærket.

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